# PRELIMINARY RESULTS TOWARD A REVISION OF THE AMARANTHUS HYBRIDUS SPECIES COMPLEX (AMARANTHACEAE) 

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#### Abstract

The present study is a review of the Amaranthus hybridus complex based on new morphological and anatomical characters. Two new combinations are proposed - A. hybridus subsp. quitensis and A. powellii subsp. bouchonii. Based on characters such as phyllotaxy, leaf traces and other morphological characters the division of the genus into subgenera is also discussed.


## RESUMEN

El presente estudio es una revisión del complejo Amaranthus hybridus basado en caracteres morfológicos y anatómicos. Se proponen dos nuevas combinaciones $-A$. hybridus subsp. quitensis y A. powellii subsp. bouchonii. También se analiza la división del género en subgéneros en base a la filotaxis, los rastros foliares y otros caracteres morfológicos.

## INTRODUCTION

The genus Amaranthus L. consists of about 70 species, of which about 40 are native to the Americas and the rest to Australia, Africa, Asia and Europe. The most frequently used infrageneric classification involves 2 subgenera and was suggested by Sauer (1955)-Acnida (L.) Aellen ex K.R. Robertson which comprises dioecious species and Amaranthus that includes monoecious species. Traditionally subgenus Amaranthus is divided in two sections, Amaranthus and Blitopsis Dumort. Recently, Mosyakian and Robertson (1996) proposed elevating the two sections of subgenus Amaranthus to subgeneric rank, subgenus Amaranthus and subgenus Albersia (Kunth) Gren \& Godr. (= section Blitopsis). Yet, they did not provide new characters to justify their revised treatment and the question of the most appropriate subgeneric classification apparently has remained open.

In spite of the fact that it has been the object of many studies, the genus Amaranthus is still poorly understood, being widely considered a "difficult" genus. Currently, the taxonomic problems are far from being clarified especially because of the widespread nomenclatural disorder caused chiefly by repeated misapplication of names. Most of the problems are concentrated in the most studied group of species, the A. hybridus aggregate. Sauer's monograph of grain Amaranths $(1950,1967)$ has solved most of the nomenclature problems and provided an extensive taxonomic treatment for the species involved. Yet nomenclature and taxonomic confusion among these closely related taxa has persisted in the literature and herbarium collections, especially in Europe. Because of such "serious nomenclature discrepancies" Jalas and Suominen (1980) were forced to present a collective map for the occurrence of "A. hybridus, A. paniculatus, A. patulus and A. powellii" in Europe. This quotation is a good example of the present confused situation. One wonders what the authors understood by "A. patulus" since it is known that this name is a synonym of A. hybridus or is sometimes comprehended as A. cruentus (Aellen 1964). The actual taxonomic concepts in this group of species-assuming that the nomenclature problems are solved-ranges between two different extremes. At one extreme is Sauer's treatment $(1950,1967)$ that recognizes as species the cultivated taxa (Amaranthuscaudatus, A.cruentus and A. hypochondriacus) and at the other is Greuter's $(1981,1984)$ who lumps the cultivated species with their putative wild progenitors (A.quitensis, A. hybridus and A. powellii respectively). All possible intermediate combinations between these two opposed treatements-many of them published since the beginning of the century by Thellung (1907, 1914, 1919) -were also used (Aellen 1959, 1964, 1972; Dostal 1950; Morariu 1952; Brenan 1961, 1981; Gusev 1972; Ehrendorfer 1973; Townsend 1974, 1985, 1988; Carretero 1979, 1985, 1990; Stace 1991, 1997; Lambinon 1992; Cherepanov 1995; etc.).

The evolutionary origins of grain amaranths are still unclear. Sauer (1967, $1976,1993)$ suggested two possible hypotheses. The monophyletic hypothesis states that the three cultivated species originated from a single wild progeni-tor-A. hybridus, followed by subsequent introgressive hybridization with two other wild species in different regions. According to this hypothesis, the first domesticated species was A. cruentus, derived from A. hybridus in Central America, followed by the domestication of $A$. hypocondriacus by repeated crossing of A. cruentus with A. powellii in Mexico and of A. caudatus by crossing with A.quitensis. The polyphyletic hypothesis suggests that each of the threegrain species was domesticated separately from a different wild species. In concordance with this hypothesis, A. hypochondriacus was domesticated in Mexico from A. powellii, A. cruentus from A. hybridus in Central America and A. caudatus from A. quitensis in South America. Detailed studies of the relationship among amaranth species using cytological or molecular methods are con-
tradictory, supporting separately both hypotheses (Pal \& Khoshoo 1972, 1973; Hauptli \& Jain 1984; Greizerstein \& Poggio 1992; Greizerstein et al. 1997; Transue et al. 1994; Lanoue et al. 1996; Chan \& Sun 1997). The taxonomic achievement of all these studies was that they proved the individuality of the taxa involved, against the lumping tendencies.

Other remaining taxonomic questions concern the status of $A$. bouchonii Thell. and A.quitensis Kunth. The first taxon is regarded as conspecific with A. powellii S. Watson by Sauer (1967), Carretero (1990), Akerroyd (1993), but is maintained at the species level by Hügin (1987), Stace (1991, 1997), Kerguélen (1993), Wilkin (1992). The second taxon, Amaranthusquitensis, was synonymised with A. hybridus by Coons $(1975,1978)$ but kept separate by almost all other authors.

This study is only the beginning of a revision of this difficult complex. Set aside for the moment are the following topics: the relationship between the closely related taxa, A. dubius Mart. and A. spinosus L. and their affinity with A. hybridus; the appropiate position of some other taxa (A. brandegei Standley, A. bigelovii Uline \& Bray, A. viscidulus Greene, A. scariosus Benth., A. lepturus S. F. Blake, A. celosioides H.B.K. and A. pallidiflorus F. Muell) and the role of hybridization and its consequences within the $A$. hybridus aggregate and among the dioecious amaranths.

Amaranthuscaudatus, together with A. hypochondriacus and A.cruentus, have created a great interest during recent years as agricultural crops in many regions of the world, due to the exceptionally high nutritional value of their seeds and leaves. Hundreds of articles document the nutritional value, the agronomical potential, genetic resources and breeding of amaranths. For a good review on the nutritional value and production methods see Kauffman and Wagoner (1984), Kauff man and Weber (1988), Kauffman (1992). For a comprehensive review on genetic resources and breeding see Brennan et al. (2000).

## MATERIAL AND METHODS

To assess anatomical variation the taxa were sampled between 1991 and 1996. Seeds collected from the wild flora or received from various Botanical Gardens were cultivated in the Botanical Garden of the University of Agronomy Bucharest, Romania. Generally 4 to 6 populations or accessions were used for each taxon involved in the study. Seedlings, young shoots, stems of different ages, mature leaves, fruits and seeds were liquid preserved in a $50-70 \%$ mixture of formalin, acetic acid and alcohol (FAA) and embedded in Paraplast or paraffin. For the study of the vascular system of the stem, plants were chosen that lacked sylleptic branching, to avoid examination of branch trace bundles. Typically stems from 25 plants, for each population were serially sectioned at 10 mm , stained with safranin and fast green, and studied with transmission and
polarized light. Furthermore, 100 seedlings for each population were grown in order to assess the cotyledon shape and the stem anatomy in juvenile stage.

Regarding the pericarp structure, fruits ranging from very young to mature were examined, but characters refer only to the latter ones. Fruits were embedded in white paraffin and transverse and longitudinal sections of 5-7 $\mu \mathrm{m}$ thickness were stained with Toluidine Blue.

The SEM study of fruits, seeds and pollen was carried on with a Hitachi S4100 SEM at 15 K V, using a Bio-Rad Sputter-Coatter SC-500. Fifty fruits and seeds were collected from each of the 50 individuals per population examined. The same number of pollen grains per taxon was used in order to assess the morphology of the pollen grains.

Morphology (without SEM) was studied using plants collected in the field in different parts of Europe and United States. Loans or other collections were examined from the following herbaria: ARIZ, B, BH, BP, BPI, BRIT, BUAG, BUC, BUCA, BUCF, BUCM, CAS, CL, CLA, CM, CRA, DAV, DS, DUKE, FLAS, I, IA, IAGB, IASI, IBE, ISC, LA, LIL, MICH, MIL, MIN, MO, MSC, NA, OKL, PRH, RB, RSA, SMU, SOM, TEX, UCR, UMO, US, UTEP, VAL, VALA, VAB, VDB, VF, WIS, Herbarium University of Agronomical Sciences Timisoara, Romania; Herbarium Faculty of Silviculture Brasov, Romania; Herbarium Natural Sciences Museum Ploiesti, Romania (not listed in Index Herbariorum).

Taking into account the confusion that prevails in many herbaria, we considered it useful to cite the typical accessions of grain amaranth species cultivated at Ames, lowa during 1984-1989, deposited now at NA (Appendix 1). Almost all these plants bear Lehmann's name and are part of the U.S. National Plant Germplast System. We often cited Sauer's specimens which were cultivated at Berkley, Davis, Madison, St. Louis or Winsconsin. In addition, we cited Grant's specimens which were cultivated at MacDonald College of Mc Gill University. In specimens citation we abbreviated: s.l. = same location and s.f. $=$ seeds from (for the cultivated specimens).

Seed samples for most amaranth species are available to future researchers from a large and diverse germplasm collection of the U.S. National Plant Germplasm System http://www.ars-grin.gov. Also, for European material we recommend Gatersleben (Germany) germplasm collection.

## Characters

Many species of the genus are greatly affected by environmental factors (nutritional elements, water availability, light conditions, injurious factors, etc.) exhibiting a great morphological variability with little taxonomic significance. An enormous number of such inconsistent states (mostly based on extremely variable characters like: plant height, branching, color of the whole plant or only of stems or petioles, abnormalities in the shape of inflorescence etc.) have received in the past various taxonomic ranks, increasing artificially the com-
plexity of the genus. For example, in Amaranthus retroflexus more than 60 varieties, forms and subforms (Thellung 1914; Priszter 1953; Morariu 1952) have been described. In the present study, besides the recognized floral characteristics, emphasis is placed on less well known characters, but ones which appear to be more stable.

Our understanding of variation in Amaranthus would improve if more care were taken in the preparation of specimens. Plants should preferably be collected when well-developed fruits and seeds are present. In addition, to improve chances of correct identification, a range of individuals from the same population and a range of flowers, fruits and seeds belonging to the same plant should be collected and examined.
Leaf and Stem.-The phyllotaxis and the courses of vascular bundles were previously studied only for A.caudatus (Gravis \& Constantinesco 1907), A.graecizans and A. hybridus (Wilson 1924). We extended these studies to the other common species of the $A$. hybridus group and to eight more species from the subgenus Albersia (Costea \& DeMason 2001). The phyllotaxis varies within the same plant: the basal leaves (from the first 4 nodes) are arranged according to a $1 / 2$ divergence. However, the phyllotaxis of the leaves from nodes 5-21( -23 ) may be regarded as constant for each species. Phyllotaxis varies within the genus, being predominantly $2 / 5$ for the species of subgenus Amaranthus and $1 / 3$ for the species of the subgenus Albersia. Towards the apex of the stem it may be $3 / 8$ in the species of the subgenus Amaranthus and $2 / 5$ in the species of the subgenus Albersia. The vascular system in Amaranthus is closed. The leaf traces consist of one large median bundle (M), two lateral (L) bundles, and, depending on the level in the stem, 2 intermediary (i) and 2-6 (1-3 orders) of marginal small bundles, $m$, m', m". The bundles within a leaf trace have a symmetrical, and characteristic, zigzag arrangement. The configuration of leaf traces can be expressed by means of a formula as follows: m" m' m L i M i L m m' m". Although the number of bundles varies along the stem, there is always a maximum number of bundles within a leaftrace that can be found at a certain level in the stem, this number being constant for each species. It varies from 11 bundles in Amaranthus caudatus, A. cruentus and A. hypochondriacus to 9 bundles in A. hybridus, A. powellii and A. retroflexus, 7 bundles in A. albus, 5 bundles in $A$. blitum, A. viridis, A. deflexus, A. blitoides, A. graecizans and 3 bundles in A. crispus. For more detailed information about phyllotaxis, the vascular system, trichomes and the anatomy of the stem in amaranths see Costea and DeMason (2001).

The general shape, the apex and the base of lamina and cotyledons were described following Hickey (1978). The leaf anatomical pattern is constant within the genus. Stomata in both upper and lower epidermis are anomocytic for all species examined-observations that disagree with Timonin (1986a,b)
who found even on the same leaf anomo-, haplo-, dia-, para-, latero-, ecycloand helicocytic stomata. The indument consists of uniseriate trichomes or mixed multiseriate and uniseriate trichomes. Lamina is dorsiventral, exhibiting "Kranz" structure, without taxonomic significance within the genus, due to lack of variability.

The Inflorescence.-The flowers are arranged in small and very contracted cymes, the first flower within each cyme, in monoecious species, being male. For this reason, young plants of dioecious species are often misidentified as monoecious species (commonly as A. hybridus or A. powellii). Exceptions to this rule are A.dubius and A. spinosus which have the male and female flowers in separate cymes (Murray 1940; Eliasson 1988). The cymes are agglomerated, axillary and additionally arranged in racemose or spiciform terminal, large and complex synflorescences. Although extremely variable, there is usually a tendency towards a morphological "type." Therefore the inf lorescence can be characterized by the number, thickness, orientation and density of branches and thus can be useful for a preliminary identification of Amaranthus species.

The Flowers.-The length of bracteoles in some species (A. hybridus and A. retroflexus) is variable and continuous, therefore without taxonomic significance. The sterile flowers of hybrids tend to be associated with longer (than normally) bracteoles (Brenner unpublished). As a result of selection, grain amaranths have usually short bracteoles, but sometimes, A. hypochondriacus may show bracteoles twice as long as the tepals, as in the wild species. The morphology of the tepals and the ratio between the tepals and the fruit provide the best technical and quick identification characteristics. The color of the mid-vein of the tepals may be green ( $A$. hybridus) or yellowish and inconspicuous ( $A$. powellii) and it can be examined on dried material (on old specimens the color fades, but generally remains visible).
The Pollen.-Erdtman (1966) defined the "Amaranthus" pollen grain type also present in other Amaranthaceae genera and even in several other centrospermous families (Nowicke 1993). The pollen grain is pantoporate, apolar, small (with $D=18-28 \mu \mathrm{~m}$ ). Generally it has more than 18 sunken pores, uniformly distributed and having the apertural membrane granulated. Tectum with granules or spinules (see also Eliasson 1988; Costea 1998a,b). Characters: the diameter of the pollen grain; number and diameter of pores; density of granules or spinules on the surface of the pollen grain according to the following scale: high $=20-30$ granules or more $/ 1 \mu \mathrm{~m}^{2} ;$ medium $=10-19$ granules $/ \mu \mathrm{m}^{2}$ and low $=2-9$ granules $/ 1 \mu \mathrm{~m}^{2}$.

The Fruits.-a. General characters as seen under $50 \times$ magnification or more (see also Klopfer \& Robel 1989a; Costea 1997b).

Fruit transverse circumscissile, indehiscent or irregularly dehiscent.-Usually
transverse dehiscence versus indehiscence is a constant characteristic, useful for species separation. In some species with normally circumscissile dehiscence (A. hybridus and to a less extent A. powellii), a transition between indehiscent, irregularly dehiscent and circumscissile fruit may be observed in the same population or even on the same plant. Other characters are: the general form of the fruit: spherical, ovoid, ellipsoidal etc.; the form of the fruit toward the stigma region: abruptly narrowed toward the stigma region, a short beak being conspicuous (A. cruentus) or fruit gradually narrowed toward the stigma region (A. hypochondriacus, A. powellii), with the apex truncate to rounded, or acute; the ratio between the length and the width of the fruit; position of the dehiscence line: in the upper half, at the middle or in the lower half of the fruit; general pattern of pericarp wrinkling; size of stigma branches: width at the base and length; position of stigma branches: erect or recurved.
b. SEM characters of fruits.-Surface of pericarp observed with the SEM at $300 \times$ magnification or more. To describe the patterns of the pericarp surface, we slightly modified the classification of Klopfer and Robel (1989a) as follows: Type A ("paniculatus" type, Klopfer \& Robel 1989a). -Cells very irregularly shaped and ramified. Principal axis of the cells not more than three times longer than the longest secondary axis. Anticlinal walls irregularly waved (Fig. 1, A, B). Type B ("bouchonii" type, Klopfer \& Robel 1989a). -Cells ramified, 4-6 times longer than wide. The anticlinal walls $\Omega$ or S-waved (Fig. l, C, D, E). Type C ("patulus" and "deflexus" types, Klopfer \& Robel 1989). -Cells less ramified or not ramified, 8-12 times longer than wide. Anticlinal walls mostly S-waved (Fig. 1, F). Type D ("albus" type, Klopfer \& Robel 1989a). -Cells less ramified or not ramified 1.5-2 times longer than wide. Anticlinal walls weekly S-waved. Type E ("lividus" type, Klopfer \& Robel 1989a). -Cells not ramified, 3-4 times longer than wide with anticlinal walls straight to $S$-waved. The delimitation of these 5 types is somehow arbitrary because with respect to pericarp surface features, the species of subgenus Amaranthus are more variable than was suggested before (Klopfer \& Robel 1989a). Almost all species examined in the hybridus complex present, even on a single fruit, a continuous transition between two types. Therefore, the character of the surface patterns should be regarded more as a tendency toward a type. Even so, in some cases it is useful to separate, for example, the subspecies of A. powellii (subsp. powellii presents the type A surface character, while subsp. bouchonii shows variation between B and C types). In the subgenus Albersia nearly all species are characterised by a unique type of surface organisation, D or E (Klopfer \& Robel 1989a; Costea 1998a).
c. Structure of pericarp.-The mature pericarp has a very simple structure, being 2-4 layered. The epicarp and endocarp are always 1-layered, while the mesocarp, according to the species, may be 1-layered (A. powellii, A. hybridus, A. retroflexus) or 2-layered (A. hypochondriacus, A. caudatus and A.cruentus).


FIG. 1. (Plate 1). Surface of pericarp in Amaranthus hybridus agg. A. Amaranthus powellii subsp. powellii; B. Amaranthus retroflexus; C.Amaranthus cruentus; D. Amaranthus hybridus; E.-F. Amaranthus powellii subsp. bouchonii.

In some cases the mesocarp originally consists of a single cell layer but finally is crushed and becomes usually no longer distinguishable (A. hybridus). As a consequence, the pericarp in these taxa is apparently 2-layered. The taxonomic importance of pericarp structure, mechanism of dehiscence and analysis of the dehiscence-indehiscence character are the object of different study (Costea, Waines \& Sanders, in ed.).

The Seeds.-The diagnostic features of the seeds were largely neglected due to their small size. Descriptions of seeds were also produced by Kowal (1954), Klopfer and Robel (1989b), Esparza-Sandoval et al. (1996) and Costea (1997c). The seeds of grain species are more variable, dark or light colored, the character being controlled by multiple alleles and additional loci (Kulakow et al. 1985; Kulakow 1987; Kulakow $\&$ Jain 1990). The following features (including the sculpture) should be observed under $50 \times$ magnification or more (Fig. 2, A): The shape of the seeds as seen from above, is variable between species but more or less constant within a species: circular, elliptic, obovate, etc. As seen laterally, the seeds usually exhibit a lenticular shape. The seeds are usually differentiated into a central, convex zone and a marginal, plane zone, exceptions to this rule being rare and diagnostic. This shape allows the seeds to float and disperse by water. The size-defined by the length of the two diameters-is constant when the plants grow in the same environmental conditions. Otherwise, variations of $0.1-0.2 \mathrm{~mm}$ from the average are possible. Appearance of the seed base, where the hilum and radicle are located: the tip of the hilum surpasses the tip of the radicle (subgenus Amaranthus, exception-A. hybridus) or the tip of the hilum is below the tip of the radicle (subgenus Albersia) (Kowal 1954; Costea 1997c). The presence between the hilum and the radicle, toward the center of the seed, of a furrow; a concavity or a concavity continued by a furrow can be also an useful additional character. The shape of the seed margin observed from profile may be acute (usually), rounded or truncated (rare). The sculpture of the seeds is the result of the concentrically distribution of the cells from the exotesta. The following variations are possible: the sculpture is evident only on the marginal zone, in the central zone being inconspicuous (usually); both the central and the marginal zone are sculptured; both the central and the marginal zone are almost smooth, and the central zone is sculptured while the marginal one is smooth or distinctly wrinkled. The color of the seeds is commonly dark-brown to blackish, or whitish-yellowish, sometimes with reddish nuances at the species cultivated as cereals. Many cultivars of A. caudatus have pink cotyledons visible through the seed coat. The color may be uniform or not in the last case usually with the marginal zone paler.

SEM characters of seeds refer to the ornamentation of the exotesta in the marginal zone of the seeds, as observed under $300 \times$, or more magnification. We used the terminology proposed by Barthlott and Ehler (1977). The aspect of


Fig.2.(Plate 2).A. Seed. General view.Amaranthus powelii subsp.powellii; B. Sculpture of exotesta on the marginal zone of the seed. Amaranthus caudatus (light coloured seed); C) Amaranthus powellii subsp. powellii; D. Amaranthus powellii subsp. bouchonii; E. Pollen. Amaranthus hybridus subsp. hybridus; F. Amaranthus hybridus subsp. quitensis.
the anticlinal (prominent or inconspicuous) and periclinal (flat, concave or convex with the sculpture of the epicuticular waxes smooth or punctiform) walls were noted.

All the above mentioned characteristics are useful for the taxonomy of the genus but difficult to use for the current identification of taxa. For this purpose we recommend the same identification keys surveyed by Brenner et al. (2000) which are mostly based on the traditional characters.

## Hybrids

Hybridization is the main source of the taxonomic problems within the $A$. hybridus aggregate. Yet the frequency of hybridization within populations and sometimes the fertility of hybrids has been over estimated (Priszter 1949, 1958). In fact, experimental hybridizations undertaken (Murray 1940; Greizerstein \& Poggio 1992) showed that such events occur infrequently and that the Fl plants have a reduced fertility (usually $80-98 \%$, rarely $60 \%$ ). The mean outcrossing rate for the cultivated species is 3.5 to $34 \%$ (Jain et al. 1982; Hauptli \& Jain 1985; Agong \& Ayiecho 1991; Espitia-Rangel 1994). Not surprisingly, considering that of ten amaranths grow in large, mixed species populations, introgression does occur, the result being formation of hybrid swarms. Hybrid plants are often difficult to ascribe to one of the species, or even to associate with the correct parental species. In the temperate regions the phenomenon commonly involves the three weedy species-A. retroflexus, A. hybridus and A. powellii. Gene flow may also occur between the domesticated species (A. hypochondriacus, A. cruentus and A.caudatus) or between the domesticated species and their wild relatives. The last situation occurs frequently in the regions where grain amaranths are cultivated and the related weed species grow in the vicinity (for example in Mexico, Ecuador, Guatemala, Peru, and Africa). In such regions the species limits blur resulting in an extremely difficult complex. Often, the pattern of variation is impossible to explain if we take into consideration only the "classical" species, suggesting that some other local (unknown ?) taxa are involved too. A possible explanation of this variability in some areas could be that outcrossing rates are higher in certain environmental conditions, depending for example on the pollinators (Hauptli $\&$ Jain 1985) and probably other factors too. It is hazardous to evaluate such plants only morphologically; detailed studies using molecular markers are necessary in the future if the consequences of hybridization are to be properly understood. However, to date molecular methods have not contributed much to the understanding of this complex of species because of their contradictory results. The attempt to evaluate the relationships between cultivated and wild amaranths, using plants possessing a degree of introgression (or even misidentified), can lead to unrealistic results and the future studies must involve careful use of both molecular and morphological methods.

The species of the subgenus Amaranthus hybridize with the species of the subgenus Acnida (Murray 1940; Sauer 1955) complicating even more the interpretation of the variability in $A$. hybridus agg. The gene pool of the grain amaranths also includes the 10 dioecious species (Brenner 1990; Brenner et al. 2000), the potential of variation being enormous. The consequence of hybridization between species of the subgenus Amaranthus and subgenus Acnida, in North America, is a subject that deserves future attention. The Fl hybrids within subgenus Amaranthus and those between species of the subgenus Amaranthus and subgenus Acnida, are of ten not strictly intermediate morphologically between their two parents, having abnormal inflorescences with very dense, crowded branches. They can easily be recognized by the great number of densely packed bracteoles that subtend the often-sterile flowers. For their accurate identification, one has to take into careful consideration what potential parent species are present in the field where the hybrids were collected. Fortunately, the species of the subgenus Amaranthus (and Acnida?) do not hybridize with the species of the subgenus Albersia (Priszter 1949, 1958).

TAXONOMIC TREATMENT
The division of the genus into three subgenera-Acnida, Amaranthus and Albersia-suggested by Mosyakin and Robertson (1996), appears to be most appropriate because it would permit revision at the section level of the heterogeneous subgenus Albersia (= sect. Blitopsis Dumort.) already started by the two authors. We support this classification with new morpho-anatomical characters. Also the fact that hybrids between the Subgenus Amaranthus and the Subgenus Albersia are unknown confirms the separation of Albersia as a subgenus.

$$
\begin{aligned}
& \text { 1. Dioecious plants } \\
& \text { 1. Monoecious plants. } \\
& \text { 2. Phyllotaxis predominantly } 2 / 5 \text {; largest leaf traces in stems with } 9-11 \text { bundles; } \\
& \text { seeds with hilum at or above the radicle level_ } \\
& \text { Subgenus Amaranthus } \\
& \text { ( } \begin{array}{l}
\text { section Amaranthus) } \\
\text { 2. Phyllotaxis predominantly } 1 / 3 \text {; largest leaf traces in stems with } 3,5 \text {, or } 7 \text { bundles; } \\
\text { seeds with hilum beneath tip of the radicle } \\
\text { ( } \equiv \text { Subgenus Amaranthus section Blitopsis Dumort.) }
\end{array}
\end{aligned}
$$

Within the subgenus Amaranthus, we support the treatment of Sauer (1950, 1967) in maintaining the cultivated taxa distinct as species from their supposed wild progenitors, supporting it with new morphological and anatomical evidence. We do not claim that combination may not be necessary in the final revision of this difficult group. However for the moment, lumping appears to be a too simple and arbitrary solution. Until the day that the variability and the relationships between all the taxa involved will be understood we consider it more appropriate to maintain them as separate species.

1. Amaranthus caudatus L., Sp. Pl. 990. 1753. Type: "Habitat in Peru, Persia, Zeylonia"; LINN 1117/26.

Amaranthus mantegazzianus Passerini, Ind. Sem. Hort. Bot. Parma 4. 1865.
Amaranthus edulis Spegazzini, Physis (Buenos Aires) 3:163. 1917.
Stout erect to arching annual up to $1-1.5(-2) \mathrm{m}$ high. Cotyledons narrow-elliptic, $13 \times 4-5 \mathrm{~mm}$, with acute apex and base; petiole about 10 mm long. Leaves rhom-bic-ovate to elliptic. Trichomes multicellular with uniseriate cells. Inf lorescence large and showy, with the terminal part $10-30(-40) \mathrm{cm}$ long, thick, pendent to erect, usually red or purplish, rarely white or yellow. Sometimes the inflorescence is similar to $A$. hybridus, consisting of many lateral, more or less perpendicular branches. Bracteoles 3-4 mm long, about 1.2-1.5 times longer than the tepals, usually not exceeding stigma branches. Tepals 5, equal, outwardly curved or erect, $1.9-2.5(-3) \mathrm{mm}$ long, obovate to broadly-spathulate, mucronate, overlapping each other, with the mid-veins uniform, yellowish-brown. Fruit circumscissile dehiscent, longer than the tepals, $1.5-2.5 \mathrm{~mm}$ long, a little longer than wide, ovoid, weakly longitudinally wrinkled, with the dehiscence line in the lower half, gradually or abruptly narrowed toward stigma region. Pericarp surface is type A. Seeds $1.3-1.5 \times 1.25-1.35 \mathrm{~mm}$, round to asymmetrically-round. Between the hilum and the radicle a furrow extends almost to the middle of the seed. The seeds are differentiated into central and marginal zones. Two distinct types of seeds exist: a) whitish-yellowish in color, ovoid in lateral view, with marginal zone smooth or irregularly wrinkled, of ten with the pink embryo visible through the seed coat, and the central zone conspicuously sculptured; the border of the seed rounded or truncated; cells of the exotesta in the marginal zone elongated ( $30-50 \mu \mathrm{~m}$ length) with prominent anticlinal walls and periclinal walls plane and verrucose (Fig. 2, B). b) dark-brown seeds, lenticular, with marginal zone sculptured and central zone smooth; uniformly colored; cells of the exotesta as in the whitish-yellowish seeds but the periclinal walls smooth; border of the seeds is acute. Pollen grains $22-24 \mu \mathrm{~m}$ with $30-40$ pores of $1.5-1.8 \mu \mathrm{~m}$ diameter. Density of granules medium. $2 \mathrm{n}=32$.

The relationships within A. caudatus were studied by Coons $(1975,1982)$ and we share that author's view of infraspecific classification.

Distribution and ecology.-In Europe, A.caudatus is grown primarily as an ornamental, and rarely escapes from cultivation in waste places. A. caudatus as a grain crop, originated at high elevations in South America, in northwestern Argentina, Ecuador, Peru and Bolivia, the closest wild taxon being A. hybridus subsp. quitensis. In the native areas you can of ten find transitional forms between the two taxa. The question remains whether A.cruentus also participated in the development of A. caudatus. Using the data from nuclear DNA and re-striction-site chloroplast variation, Lanoue et al. (1996) found that A. caudatus and $A$. cruentus are more closely related to each other than to their respective
putative progenitors. Chan and Sun (1997) stated also that A. caudatus is more closely related to A. cruentus, and both of them nearer to A. hybridus than to A. quitensis. These data are not confirmed by cytological studies (Pal \& Khoshoo 1972, 1973; Hauptli \& Jain 1984; Greizerstein \& Poggio 1992; Greizerstein et al. 1997). Also, other mollecular studies, using RAPD markers indicate that $A$. caudatus is more closely related to A. hypochondriacus than to A. cruentus (Transue et al. 1994). Sauer (1967) stated that when growing together with the other two cultivated grain species, A. caudatus does not usually form hybrids and crossing barriers in A. caudatus have also been observed by Coons (1975, 1982). However, among the accessions cultivated at Ames, Iowa between 19841989 and deposited at NA, many of the plants impossible to ascribe to a definite species were obviously related morphologically to A.caudatus. In all cases such plants have obovate to spathulate tepals, only partially overlapping each other, and narrower than in typical A.caudatus but wider than in any other species, suggesting a degree of introgression. Two morphologic types are commonly encountered:

1) The plants from Morelos, Mexico identified as "A cruentus" by Lehmann or "A. hybridus subsp paniculatus" by Spjut, apparently represent a definite land race probably involving A. cruentus and A. caudatus [(Spjut 8808, 8810, 8821; Lehmann: AMES 5501 (Type 1 and 2), 5502, 5179, 5182, 5183, 5188, 5193, 5195, 5196, 5197 (Type l and 2) 5198(Type l and 2), 5200, 5201, 5202, (NA)]. Besides this recognizable type, many other accessions bear morphological "traces" of A. caudatus but there are more heterogenous suggesting either the participation of A.cruentus or A. hypochondriacus, or both, in their origins.
2) The plants from Ecuador identified as "A. hybridus" by Lehmann or "A. hybridus subsp. quitensis" by Spjut, probably involve A. caudatus and A. hybridus (Ecuador, Lehmann, PI 490663, PI 490664, PI 490666, PI 490667, PI 490670, PI 490716, PI 490718, PI 490719, PI 490722, PI 490672, PI 490715, PI 490723, PI 490724, PI 490725, PI 490726, PI 490728, PI 490730, PI 490731, PI 490732, PI 490735, PI 490737, PI 490742, PI 490746, PI 490747, PI 490748, PI 490752. These specimens are different from the red Ecuadorian "sangorache," another example of taxonomic incertitude in grain amaranths. Sauer included it within A. quitensis and Brenner et al. (2000) suggest the same. Coons accepted it as a variety of A. hybridus (s.l, including. A. quitensis) (1975, 1978). As noted by Coons, even if closely related to A. caudatus and A. hybridus (incl. A.quitensis) and to a less extent with A.cruentus, "sangorache" presents some unique features such as the tepals position and the form of the fruits. We also think that it deserves separate recognition-at least as a variety (if not as a subspecies)-but its position in relation within the species complex requires further investigation.
Representative specimens examined.AFRICA.ETHIOPIA. Harege Prov.: Harar, escaped from cultivation, $9^{\circ} 5^{\prime} \mathrm{N}, 42^{\circ} 17^{\prime} \mathrm{E}, 7$ Sep 1963, Burger 3237 (US). 20 km from Harar Leprosarium "Besadimo," 1425 m, 3 Aug 1967, E. Westphal \& Westphal-Stevels 994 (MO). Illubabor Prov.: 8 km SW Teppi, $7^{\circ} 9^{\prime} \mathrm{W}$,
$35^{\circ} 18^{\prime} \mathrm{E}, 1300 \mathrm{~m}, 9$ Dec 1964, Meyer 8995 (NA). Kefa Prov.: E of Jima, Oct 57, Anderson s.n. (WIS). Shoa Prov.: Addis Abeba, Hugh Rouk, 12 Jan 1965, Meyer 9093 (NA). KENYA. Eastern Prov.: Mount Kenya, 3630 m, 21-27 Sep 1909, Mearns 1377 (A). SOUTH AFRICA: Pretoria-Riviera, cultivated, 1 Jun 1964, Schliechen 9983 (A).

ASIA. ISRAEL: Sharon Plain, Herzliyah, near Yarkon bridge, 21 Apr. 1935, Eig, Zohary \& Grizi 730 (A, BH,FLAS, MO, NA). NEPAL: s.f. Marku Valley, Sirsagarhi,"grain crop," 30 Jan 1951, Sauer 1505C (WIS). s.f. the SW Slopes of Annapurna, "cultivated as grain," $28^{\circ} 20^{\prime} \mathrm{N}, 83^{\circ} 45^{\prime} \mathrm{E}, 2000 \mathrm{~m}, 1$ Nov 1954, Sauer 1776 (WIS). PAKISTAN. Ladak Prov.: Indus Valley, Leh to Kaltse, 12-14 Jul 1856, Schlagintweit 1486 (GH). INDIA: s.f. unknown locality, collected in Aug 1910 and cultivated at New York, Arnold s.n. (BH). Tamil Nadu: s.f. Madras, 23 Sep 1964, Sauer $3964 b$ (NA, WIS); s.I., 30 Aug 1964, Sauer 3962 (MO, NA, WIS); s.l., 16 Sep 1964, Sauer 3964 a (WIS). CHINA: s.f. Yunnan, 3 Sep 1940, Cowgill 2087 (BH). s.f. Mowhsien, Szechwan, 2000 m, "cultivated crop," 9 Jan 1950, Sauer 1503 A (WIS). JAPAN. Hondo: Tokyo,"cultivated," 26 Oct 1959, Makino 11254 (CAS).

EUROPE. SWEDEN. Stockholm: s.f. Stockholm, Botanical Garden, Grant 219 (WIS). ENGLAND: s.f. unknown locality cultivated at New York, Ithaca, 7 Aug 1960, Bailey 8417 (BH). FRANCE. Doubs: s.f. Besancon, Botanical Garden of the University of Besancon, Grant 218 (WIS).Loire-Atlantique: s.f. Nantes, Botanical Garden of Nantes, Grant, 216,217 (WIS). ROMANIA. Constanta Co.: Medgidia, "cultivated as ornamental and ruderal," 15 Sep 1995, Costea s.n. (BUAG).

NORTH AMERICA.UNITED STATES: CALIFORNIA. Santa Barbara Co.: Santa Barbara, 22 Jan 1958, Pollard s.n. (CAS). San Bernardino Co.: Rialto, 1 Oct 1933, Wheeler 2141 (DS). Ventura Co.: Casitas Pass Rd., Foster Park, 23 Oct 1965, Pollard s.n. (CAS). Santa Clara Co.: Palo Alto, 22 Jan 1958 Pollard s.n. (CAS). 18 Sep 1968,McClintock s.n. (NA).FLORIDA. Alachua Co.: Gainesville, 14 Sep 1953, West s.n. (FLAS). ILLINOIS. Chicago (cultivated), 13 Jul 1958, Pollard s.n. (DUKE, FLAS); s.I., 13 Jul 1987, Plowman 14507 (US). MINNESOTA. Stearns Co.: St Cloud, 807 S, $6^{\text {th }}$ Avenue, 26 Sep 1991, Lindstrom 1991 (KSC). NEW YORK. Tompkins Co.: Ithaca, 28 Sep 1936, Allen 6391 (BH); s.l., 11 Sep 1914; s.I., 29 Jul 1920; s.l., 20 Oct 1920; s.l., 17 Sep 1924; s.I., 23 Jul 1928, Bailey s.n. (BH); s.l., 3 Aug 1948, Dress 1405 (BH,NA);s.I., 31 Aug 1948, Dress 1232 (BH,NA). VIRGINIA. Buchanan Co.: Upper Prater, 11 Aug 1988, Churchill 88234 (MSC). WISCONSIN. Dane Co.: Madison, Oct 1924, Davis s.n. (WIS).

SOUTH AMERICA. PERU. Dep. Ayacucho: Prov.Cercado,Ayacucho, 2800 m, 10 Mar 1964,Gade s.n. (WIS).Dep. Cuzco: Urubamba, 21 Apr 1915, Cook \& Gilbert 256 (NA). Paruro, 10 May 1964, Gade s.n. (WIS). Dep. Huancavelica: Mejorada, 31 Oct 1948, Saver 1283D (WIS). BRASIL. Mun. Curtiba: Parana, "ornamental," 26 Jul 1980, Kammrow 1368 (WIS). BOLIVIA. Prov. Cochabamba: Cochabamba, 31 Oct 1948, Sauer 1241, 1333, 1303 (DAV, DS, GH, NA, WIS);s.l., 12 Dec 1948, Sauer 1179 (MO, DAV, DS, GH, MO, NA, WIS). s.f. Cochabamba, grown at Botanical Garden Illinois, March-May 1948, Fuller s.n. (NA). Prov. La Paz: s.f. Sacaba, 19 Nov 1959, Sauer 2540 (NA, WIS). s.f. Tajma, 17 Dec 1959, Sauer 2542 (NA, WIS).s.f. Chulumani, Nov 1959, Sauer 2539 (WIS). ARGENTINA: cultivated, 20 Apr 1942, Hunzinker 2083, 2083 Bis (BH). Prov. Salta: Dep La Vina, Puerto de Dias, cultivated, 1200 m, 1941, Hunzinker 1321 (A).
2. Amaranthus cruentus L., Syst. Nat.ed. 10, 1269. 1759. (Fig. 3). Type: "CHINA"; LINN 117/19. A. hybridus L. subsp.cruentus (L.) Thell. var. paniculatus (L.) Thell., Fl. Adv. Montpell. 205.1912. A. hybridus L. subsp.cruentus (L.) Thell. proles paniculatus (L.) Thell., Ascherson \& Graebner, Syn. Mitteleur. Fl. 5:247. 1914. A. hybridus L. subsp. paniculatus (L.) Hejny, Dostal, Kvetevna CSSR. 444. 1950. A. hybridus L. subsp. incurvatus (Tim. ex Gren. \& Godr.) Brenan var. cruentus Mansf., Die Kulturpflanze 2:54. 1959.

Amaranthus paniculatus L. Sp. Pl. ed. 2, 2:1406. 1763.
Amaranthus sanguineus L. p.p., Sp. Pl. ed. 2, 2:1407.1763.
? Amaranthus chlorostachys Willd., Hist. Amaranth. 34.1790.
Erect annual 0.5-1.5 m, usually reddish throughout. Cotyledons lanceolate to narrow-ovate, $16 \times 5-6 \mathrm{~mm}$, with rounded apex and cuneate base; petiole about


Fig. 3. Amaranthus cruentus, from Lehmann, AMES 5602 (NA).

7 mm long. Leaves rhombic-ovate to broadly-lanceolate, 4-15 $\times 2-18 \mathrm{~cm}$. Trichomes multicellular with cells uniseriate. Inflorescence usually with many lateral, perpendicular, thin branches. Bracteoles $2-3 \mathrm{~mm}$ long, equalling or slightly longer than the tepals. Tepals 5, almost equal (one is approximately 0.5 mm longer than the other 4), oblong, acute, with the mid-veins uniform, yel-lowish-brown. Fruit circumscissile dehiscent, 2-2.5 mm long abruptly narrowed toward the stigma region, a short, thin rostrum being evident. Fruit about 1.5 times longer than wide, obovate to rhombic, 2-2.5 mm long, with the dehiscence line at the middle or in the upper half. The pericarp is almost smooth or weakly wrinkled above the dehiscence zone. Type of pericarp surface variable: A to B. (Fig. 1, C). Seeds obovate to elliptic-asymmetrical $1.25-1.6 \times 1.1-1.2 \mathrm{~mm}$, whitish or yellowish, rarely dark-brown. The pale seeds are very much like the ones described for $A$. caudatus. The differences are that the furrow between the hilum and the radicle is prolonged only about $1 / 3$ of the way through the diameter of the seeds and that the pink tint is usually absent. The dark seeds exhibit a concavity above the hilum and have both the central and the marginal zone (especially) sculptured. The cells of the exotesta as in $A$. hybridus. The border of the seed is acute. Pollen grains $20-25 \mu \mathrm{~m}$, with 33-45 pores of 1.9-2.1 $\mu \mathrm{m}$; density of spinules medium. $2 \mathrm{n}=32,34$.

Distribution and ecology.-Apparently originated in Central America from the wild species A. hybridus, as a grain crop. Sauer (1950) and Sanchez-Del Pino, Flores Olvera and Valdes (1999) noted transitional forms between the two species in Mexico but such examples also occur in Central America and Africa. Together with the other two grain amaranth species, it was introduced into the Old World by the Spaniards and then into Asia and Africa. Today it is cultivated worldwide, mostly as a garden ornamental. In United States, South America, Zaire, Sierra Leone, Ethiopia, India and Middle East it is cultivated as a cereal and in many other countries it is being evaluated experimentally for this purpose. The commercial grain amaranth crop involves both A. cruentus and A. hypochondriacus as well as hybrids between the two. In Africa A.cruentus is also cultivated as a potherb, bearing the name "African spinach" or "Sudan spinach," or is used as animal fodder. The leaves have a high content of protein and vitamins. This species sometimes escapes from cultivation in ruderal places.
Representative specimens examined:AFRICA. EGYPT: Bashtil, 21 Oct 1974, Mosein \& Riad Higazy 18 (MO). ETHIOPIA: Road from Arba Minch to Soddo, 108 km from Arba Minch; $1180 \mathrm{~m}, 7$ Feb 1968, E. Westphal \& J.M. C. Westphal $323 b$ (US). NIGERIA. State North East: Distr. Gembu, Mobilla Plateau, 10 May 1972, Gbile et al. 1337 (MO). CAMEROON. Prov. Sud-Ouest: Dep. Fako, Bakingili, $4^{\circ} 04^{\prime} \mathrm{N}, 9^{\circ} 02^{\prime} \mathrm{E}$, 0-30 m, 12 Jun 1984, Thompson \& Rawlins 1383 (MO, CM). Nkoubisson, Collection Garden of Department of Agriculture ENSA, 17 Dec 1976, J.M.C. Westphal 7375 (NA); s.I., 18 Dec 1976, J.M.C. Westphal 9010 (NA). UGANDA. Distr. Kampala City: Botanical Garden of Makerere University, $0^{\circ} 17^{\prime} \mathrm{N}, 32^{\circ} 34^{\prime} \mathrm{E}$, 1200 m, 27 Feb 1972, Katende 1735 (MO). KENYA: s.f. unknown locality cultivated at Miami,Florida, 7 Sep 1920, Shantz 51847 (BH). ZAIRE (CONGO). Distr. Shaba: 15 km of Lubumbashi, 22 Dec 1961, Schmitz 7522 (MO). BURUNDI. Distr. Bujumbura: Bujumbura, 780 m, 15 Sep 1974, Auquier 4090
(MO);5.l., 800 m,May 1978,Lambinon 78/388 (MO). Rushubi, $3^{\circ} 22^{\prime} \mathrm{S}, 29^{\circ} 28^{\prime} \mathrm{E}, 1650 \mathrm{~m}$, Mar 1981, Reekman 9612 (MO). SOUTH AFRICA. Eastern Cape: Grahamstown, cultivated, 2400 m, 30 Jul 1972, Bayliss 1377 (BH).

AUSTRALIA AND OCEANIA. PAPUA NEW GUINEA: East Highlands Distr.: Norey Kora Swamp, $6^{\circ} 30$ S, $145^{\circ} 75^{\prime} \mathrm{E}, 1400$ m, cultivated, Oct 1966, Wheeler \& Anu 5857 (A).

ASIA. INDIA: s.f unknown locality cultivated at New York, Ithaca, 15 Aug 1933, Gilmore 13600, 15595 (BH).Pembra, Malabar Wynsod, Millet's Garden, 800 m, 16 Apr 1963, Noble \# O (NA, WIS). CHINA. Kwangsi: near San-t'ai-ling, 28 Aug 1937, Taam Ying-Wah s.n. (BH). VIETNAM. Annam (Trung Phan region): Tourane (Da Nang), Jul 1927, J. Clements \& M. S. Clements 3309 (US). PHILIPPINES. Mindanao Island: Davao, Apr 1903, DeVore \& Hoover 112 (US). INDONESIA. Holmahera Island: Kampung, Pasir Putih, cultivated, 13 Feb 1981, Taylor NM-III P704 (A). E Coast: Vicinity of Loemban Ria, Asahan, 5 Feb12 Apr 1934, Bocea 8022 (US). Adian Rindang, vicinity of Hoeta Tomoeau Dolok, 17 Nov-10 Dec 1935, Bocea 8710 (A).

AUSTRALIA. New South Wales: Summer Hill,"spontaneous in garden,"May 1970,Michael M8 (WIS).

NORTH AMERICA. UNITED STATES. ARIZONA. Navajo Co.: s.f. Hotevilla, Hopi Indian Reservation, 6 Nov 1950, Sauer 1343 E (WIS); s.I., May-Aug 1959, Sauer 2530 (WIS). ALABAMA. Jefferson Co.: Birmingham, ruderal, 4 Oct 1968, Kral 33646 (SMU). CALIFORNIA. San Bernardino Co.: San Gabriel Mountains, San Antonio Canyon, Chapman Ranch above Mountain Baldy Village, 1300 m, Thorne \& Thorne 191074 (RSA). Santa Clara Co.: Stanford University, 28 Oct 1896, Dudley 24899 (SMU). Palo Alto Harbor, ruderal, 11 Aug 1974, Thomas 17504 (DS). Palo Alto, along Alma Street, near Channing Street, 27 Sep 1961, Thomas 9791 (CAS,DAV). San Joaquin Co.: Calaveras River bottom, 17 Sep 1927, Stanford 170585 (DS). KENTUCKY: unknown locality, cultivated, 1817, Short s.n. (NA). MICHIGAN. Ingham Co.: near Lansing (ruderal), 13 Oct 1866, Bailey s.n. (BH). MISSOURI. Boone Co.: Columbia, "ruderal," 18 Aug 1933, Dimes 983 (UMO). East Higlands, ruderal, 9 Aug 1933, Dimes 921 (UMO). NEW YORK. Albany Co.: near Londonville (ruderal), 12 Sep 1932, Muenscher 17858 (BH); s.l., 23 Sep 1928, Burnham 17206 (BH). PENNSYLVANIA. Allegheny Co.: N side of Pittsburgh, ruderal, 4 Aug 1946, Buker s.n. (CM). Bucks Co.: West Bristol, ruderal, 17 Jul 1952, Long 75306 (CM). WISCONSIN. Dane Co.: Madison,"waste ground," Oct 1938, Shinners s.n. (WIS). HAWAII. Honolulu Co.: Aina Haina, 27 Oct 1978, Bush 939 (US, NA).

CENTRAL AMERICA AND GREATER ANTILLES. MEXICO. CHIAPAS.: Bonifilo Ocosingo, 26 Nov 1976, Calzad et al. 2869 (WIS). JALISCO.: Mpio. De Cuantilan, $19^{\circ} 28^{\prime} 13^{\prime \prime} \mathrm{N}, 104^{\circ} 11^{\prime} 04^{\prime \prime} \mathrm{W}, 750 \mathrm{~m}, 28$ Aug 1991, Cevallos et al. 140 (SMU). MICHOACAN.: Patzcuoro, 2050 m, 20 Oct 1979, Caballero 1106 (WIS); s.l., 14 Oct 1949, Caballero 1059 (WIS). OAXACA.: s.f. Jicatepec, Aug 59, Sauer 2529 (WIS). PUEBLA.: s.f. Acatlan, 30 Oct 1948, Sauer 1278 (GH, MO, NA, UC, WIS). CUBA. Ciudad de la Havana: Havana, Estacion Central Agronomica, cultivated, Baker 2843 (GH). HAITI. Tortuga Island, Vicinity of la Valle, 3 May 1929, E. C.Leonard \& G.M. Leonard 15302 (US). GUATEMALA. Dep. Alta Verapaz: Coban, 2 Nov 1950, Sauer 1265-F (WIS). Cubilquitz, 350 m, Aug 1903, Tuerckheim s.n. (GH). Dep. Chimaltenango: s.f. Chimaltenango, 28 May 1948, Sauer 1168 (MO, NA, WI); s.I., Sauer 1159, 1183 (DAV, NA); s.I., Sauer 1184,1178 (DS, GH, UC, NA, WIS); s.I., 10 Oct 1948, Sauer 1267,1240 (MO, NA, WIS); s.I., 31 Oct 1948, Sauer 1240, 1279 (MO,WIS, NA); S.I. and same date Sauer 1276, 1159, 1129, 1264, 1305, (DS, GH, NA, UC, WIS); s.I. and same date Sauer 1323, 1296 (DAV, NA, UC); s.I., 20 Nov 1948, Saver 1373, 1374 (MO, NA, WIS); s.l. and same date Sauer 1367 (NA); s.I., 9 Dec 1948, Sauer 1380 (MO, WIS, NA); s.I., 23 Dec 1948, Sauer 1240 (DAV, MO, NA, WIS); s.I., 1 Feb 1949, Sauer 1949 (MO, NA, WIS). s.f. San Juan Sactepequez, 18 Oct 1948, Sauer 1177 (NA, DAV); s.I., 30 Oct 1948, Sauer 1322, 1269, 1286, 1176, 1321, 1275, 1265 (NA, UC, WIS); s.I., 6 Nov 1948, Sauer 1265 (DAV, UN); s.I., 20 Nov, Sauer 1369, 1176 (DAV, UN). NICARAGUA. Rivas: Isla Ometepe, Volcan Maderas, $11^{\circ} 27-28^{\prime} \mathrm{N}, 85^{\circ} 31-32^{\prime}, 400-800 \mathrm{~m}, 24$ Sep 1984, Robleto 1273 (MO). EL SALVADOR: San Salvador, cultivated, Jun 1922, Calderon 739 (GH). 20 Dec 1921-4 Jan 1922,"weed in garden," Standley 19238 (GH, US).

SOUTH AMERICA. VENEZUELA: Bolivar, on the Orinoco, 75 m, Feb-Mar 1921, L. H. Bailey \& Z.

Bailey 839 (BH). COLOMBIA. Dep. Antioquia: Robledo, 1560 m, 12 Sep 1965, Grisales 11 (US). Dep.
Cesar: Becerril, Jul 1970, Ruddle s.n. (WIS). PERU. La Liberdad:Trujillo, Hacienda la Encalada, 2300 m, 13 Feb 1957, Sagastegui 38 (US). BRASIL. Distr. Federal: Paranoa at Lagoa Paranoa Lake, 12 Dec 1965, Irwin et al. 11239 (MO). Distr. Santa Catarina: Florianopolis, 20 m, 8 Aug 1964, Klein 5353 (US).
3. Amaranthus hybridus L., Sp. Pl. 990. 1753. Type: "Habitat in Virginia"; LINN 1117/19.

Annual to 0.5-1.5(-2) m, usually erect. Stems weakly to densely pubescent above, multiseriate hairs being mixed with uniseriate hairs. Leaves rhombic-ovate to broadly-ovate-lanceolate. Inflorescence dark-green, either with many crowded slender, lateral branches, or lax, with only a few flexuous branches. Bracteoles $2.5-4(-6) \mathrm{mm}$ long, narrow, about $1.2-1.5$ to 2 times longer than the tepals. Tepals 5 , almost equal, or one of them longer, $1.5-2.5(-3) \mathrm{mm}$ long, with the mid-vein dark-green, with very variable form and length: a) narrowly-ovate to oblonglanceolate, acute to subacute, erect, shorter than the fruit or b) oblong-lanceolate, obovate to spathulate, erect to outwardly curved, equal to longer than the fruit. Fruit usually circumscissile dehiscent, 1-1.5 times longer than wide, with the dehiscence line at the middle or in the upper half, more or less abruptly narrowed toward the stigma region and coarsely wrinkled above the dehiscence line. Infrequently plants with indehiscent or irregularly dehiscent fruits may be also encountered. Stigma branches are short, slender, erect ( $0.9-1.4 \mathrm{~mm}$ length and $0.1-1.18 \mathrm{~mm}$ width at the base). Type of pericarp surface variable: B to C (Fig. 1D). Seeds $1-1.4 \times 1-1.35 \mathrm{~mm}$, broad-elliptical to circular, lenticular. The tip of the hilum is placed below or at the same level as the tip of radicle. Seeds differentiated into central and a marginal zones, both sculptured. The cells of the exotesta are polygonal, $25-35 \mu \mathrm{~m}$, with prominent anticlinal walls and convex, finely sculptured periclinal ones. The border of the seed is acute. Color dark brown to black, sometimes with the marginal zone having a paler tint.

Amaranthus hybridus is an extremely variable species, especially in Mexico, Central and South America and Africa (see also Sauer 1950). Coons (1975, 1978), after a meticulous study of their relationships, considered A. quitensis a synonym of $A$. hybridus. However she admited that one character, the inner tepal index, may be significant though not correlated with other characters. The description by Kunth (1817) of the pistilate flowers of A. quitensis: "calyx quinquepartitus; laciniis lanceolato-oblongis, obtusis" is actually a better description of A. hybridus. Thellung (1914) amended the description of A. quitensis: "tepals 5, about 2 mm long, spathulate with the apex broad-rounded (with mucro), with a green mid-vein continued into the mucro. Fruit shorter (rarely as long as) than the perianth." We consider that both descriptions together are more likely to represent A. quitensis. These features induced Bolos and Vigo (1974) to include A.quitensis as a subspecies of $A$. retroflexus. However, the real affinities of $A$.quitensis are more with $A$. hybridus, in which we include it as a subspecies. The hybrid between subsp. hybridus and subsp. quitensis has a pollen viability of $60 \%$ (Greizerstein \& Poggio 1992), a value that shows both the
affinity and the distinctness of the two taxa. Also, Greizerstein et al. (1997) showed significant differences in karyotype formulae and asymmetry indexes between the two taxa. Molecular evidence for the distinctness of the two taxa was provided by Chan and Sun (1997). We find the pollen of the two subspecies of $A$. hybridus easy to differentiate.

Amaranthus hybridus (especially subsp. quitensis) stands apart from Amaranthus powellii and A. retroflexus in its ecology and in its flowering and fruiting times in temperate regions, being about 2-4 weeks later. Native to Eastern North America, Mexico, Central and South America, but now a widespread and noxious ruderal and segetal weed.

1. Cotyledons narrow-elliptic to elliptic with rounded or obtuse apex; most tepals narrowly-ovate to oblong-lanceolate, acute or subacute, erect, shorter than the fruit; tectum with medium density of granules $\qquad$ A. hybridus subsp. hybridus
2. Cotyledons lanceolate, with acute apex; most tepals spathulate to obovate, obtuse or truncated, almost erect or outcurved, longer (rare equal) than the fruit; tectum with high density of spinules
A. hybridus subsp. quitensis

3a. Amaranthus hybridus subsp. hybridus (Fig. 4).
Amaranthus patulus Bertol. Comment. Itinere Neapol. 19. 1837. A. hybridus L. subsp. patulus (Bertol.) Carretero var. patulus, Collect. Bot. (Barcelona) 11:127. 1979. A. hybridus L. subsp. cruentus(L.) Thell. var patulus. (Bertol.) Thell., Fl. Adventice Montpell. 8:206.1912. A. hybridus L. subsp. hypochondriacus (L.) Thell. "proles" cruentus (L.)Thell. var. patulus (Bertol.) Thell., Ascherson \& Graebner, Syn. Mitteleur. Fl. 5:244. 1914.
Amaranthus incurvatus Tim. ex Gren. \& Godr., Prosp. Fl. France 8. 1846. A. hybridus L. subsp. incurvatus(Tim. ex Gren. \& Godr.) Brenan var. incurvatus, Watsonia 4:268, 1961.
Amaranthuschlorostachys auct., non Wild.
Cotyledons narrow-elliptic to elliptic, $10-12 \times 4 \mathrm{~mm}$, with rounded or obtuse apex. Pollen grains 22-28 $\mu \mathrm{m}$ with $25-35$ pores of $1.4-1.6 \mu \mathrm{~m}$ in diameter. Density of granules medium. (Fig. 2, E). $2 \mathrm{n}=32,34$.

The name $A$. hybridus was rejected as ambiguous by some authors because it was widely and persistently misapplied to A. powellii or A. hypochondriacus. As all these species were clearly typified, we cannot follow such a view. Another name "A.chlorostachys" which was very much used to designate this taxon, is based on a single green plant, within a red-coloured population of cultigens from India (A. paniculatus WILLD 17521(B)). It appears that Willdenow described this mutant as a separate cultigen, which later authors, ambiguously but constantly synonymized either with $A$. hybridus or with A. powellii (especially in Europe).

Sauer (1950) distinguished a "northern race" and a "tropical race" of A. hybridus. We subscribe to this practical, non-systematic grouping. The northern race is the "typical" A. hybridus, a common weed in the temperate regions of the world that causes little taxonomic problems. Sometimes introgression with $A$. retroflexus, A. powellii or dioecious species has been documented, but usually individuals are easy to identify. The length of bracteoles and the inflorescence


FIG. 4. Amaranthus hybridus subsp. hybridus, from McWilliams 15123 (IA)
are variable, continuous and not correlated. Consequently, further infraspecific separation of a var. (subsp.) "hybridus" with bracteoles about 2 times longer than the tepals and inflorescence dense with many lateral crowded branches, and a var. (subsp.) "patulus" with bracteoles about $1-1.5$ times longer than the tepals and an inflorescence less ramified and more lax, seems arbitrary.

The variability of the "tropical race"-common in Mexico, South America and Africa-is on the other hand exceptional, suggesting in our view that sometimes, additional taxa (unknown or other than the ones examined in this study) have contributed to the variability. Of ten these plants can be named A. hybridus only in a broad sense. If we use the tepal length character, such plants fall again into the two categories; a) plants with flowers that have the tepals longer than the fruit, and b) plants with flowers that have the tepals equal or shorter than the fruit. Within the first category, we encountered among plants from Mexico a distinctive variation that might deserve taxonomic recognition. It resembles subsp. quitensis but is obviously different, with tepals acute, mucronate, recurved, and up to 2 times longer than the fruit. Such plants were identified by Sauer as "A. scariosus $\times$ A. hybridus ?" or "A. hybridus, atypical" and were also observed and cited by Sanchez-Del Pino et al. (1999). Examples:

Chiapas: Municipio of Venustiano,Carranza, 25 Oct 1966, Laughlin 2699 (DUKE). Durango: Oct 1896, Palmer 759 (GH). Hidalgo: Rio Tula, 1700 m, 15 Mar 1965, Quintero 2673 (DS). Oaxaca: Valley of Oaxaca, $1560 \mathrm{~m}, 8$ Jul 1897, Pringle s.n. (CM, IA, MICH, MIN). 15 km SE of Oaxaca, 1740 m , 1 Oct 1962, Ugent \& Flores 2628 (WIS); Upper slopes of Cerro San Felipe, $17^{\circ} 9^{\prime} \mathrm{N} 96^{\circ} 50^{\prime} \mathrm{W}, 3$ Oct 1962, Ugent \& Flores 2706 (WIS). Chimalapa, $1100 \mathrm{~m}, 16^{\circ} 42^{\prime} \mathrm{N} 94^{\circ} 05^{\prime} \mathrm{W}, 23$ Oct 1984, Maya 763 (MO); $16^{\circ} 43^{\prime} \mathrm{N} 94^{\circ} 08^{\prime} \mathrm{W}, 14$ Nov 1984, Maya 899 (MO). Tamaulipas: San Jose, 20 Feb 1939, Le Sueur 112 (ARIZ).

The plants from the second category are even more variable suggesting, in our view, the participation of other taxa than A. powellii, A. cruentus or (and) A. hypochondriacus. Besides the "typical" variation of Amaranthus hybridus, we have encountered the following situations:

1) Plants reddish throughout.
2) The inflorescence composed of lax monochasial cymes (ripidium) with the rachis and the secondary axes visible (usually cymes in Amaranthus are very contracted and such details cannot be easily observed). Such lax cymes may be arranged in thick spiciform inflorescences, resembling A. powellii or in very branched inflorescences, with many patent, lateral branches (as in typical A. hybridus).
3) The bracteoles extremely thin, acicular, spinescent, rigid, 2-4(-5) times longer than the flowers.
4) The bracteoles arranged more or less at right angles to the main branches of the inflorescence, giving a general bristly appearance.
5) The bracteoles strongly recurved.
6) Variable number of tepals, $3-5$, membranous, very unequal, without green mid-veins.
7) Tepals spathulate to obovate.
8) Tepals reduced, very small.
9) Variable number of stames, $3-5$.
10) Fruit spherical, indehiscent, irregularly dehiscent or circumcissile with the pericarp smooth, the apex rounded (without a "beak") and the stigma branches very thin and erect.

The plants may exhibit one or more of the above characteristics, sometimes in combination with the usual features of $A$. hybridus. The variation is continuous, and at least for the moment, it was impossible to classify it into distinct types. As Sauer suggested (1950), collecting more material from these regions is needed for a better understanding of this taxon.

Distribution and ecology.-Originally from Eastern North America, Mexico and Central America, but now widespread all over the world as a weed in cultivated or waste places.
Representative specimens examined. AFRICA. ALGERIA. Tilimsen: vicinity of Tlimsen, $250 \mathrm{~m}, 24$ Aug 1932,Faure s.n. (US). ZIMBABWE. Mashonaland East: Salisbury City (Harare), 3 Mar 1979, Bayliss 8999 (MO). Que Que Distr.: Silsbury, 15 Mar 1978, Chipunga 165 (MO). MALAWI: Ulongue, Zone A, 17 Oct 1985, Patel \& Bauda, 2799 (MO).

ASIA. PAKISTAN. Azad Kashmir: Mazaffarabad Distr., 4 Oct 1975, Chaudhri et al 320 (MO). Punjab: Rawalpindi Distr. Islamabad, University of Islamabad, $2200 \mathrm{~m}, 2$ Sep 1975, Chaudhri et al. s.n. (CM). Swat: Marghazar, 1300 m, 14 Oct 1975, Shah et al 501 (A). CHINA. Huanan: Cili, 390 m, 9 Sep 1984, Chow et al 395 (A). JAPAN. Honshu: Pref. Kyoto, Goma, Hiyoshi-cho, Funai-Gun, 200 m, 29 Sep 1991, Murata \& Takahashi 70295 (A). Miyagi: Miyagino-mushi, 3 Oct 1972, Naito 72103 (A, MO). Musashi: Tokyo-to, Hondo, 22 Oct 1960, Furuse s.n. (A).

AUSTRALIA AND OCEANIA. AUSTRALIA. New South Wales: Woolloomooloo, $33^{\circ} 52^{\prime} \mathrm{S}$, 151¹3'E, 6 Apr 1976, Coveny 7788 (A, RSA). Summer Hill, May 1970, Michael M9 (WIS). Queensland: Brisbane, Kingaroy, 15 Apr 1947, Smith 3027 (A).

EUROPE.SWITZERLAND. Basel: Klein Riechen, 10 Sep 1932,Aellen s.n. (WIS).SPAIN. Catalunya: Barcelona, Can Tunis, 23 Sep 1913, Sennen 1789 (GH). ITALY. Prov. Modena: Formigine, Aemilia, 22 Sep 1917, Fiori \& Beguinot 2428 (BH,GH). Prov. Turin: La Molineta, 11 Sep 1852, Perrier de la Bathie s.n. (GH).ROMANIA. Mun. Bucharest: near Bucharest, 75 m, 26 Sep 1971, Morariu 3334 (CM). Bucharest, Campus of the University of Agronomic Sciences, 12 Sep 1994, Costea s.n. (BUAG).

NORTH AMERICA. CANADA. Lambton Co.: Squirell Island, 2 Oct 1957, C \& L.O. Geiser 893 aSq (WIS). UNITED STATES. ALABAMA. Dallas Co.: 5 mi E of Selma, $35 \mathrm{~m}, 23$ Sep 1965, Demaree 52967 (SMU,WIS). Lamar Co.: 7 mi N of Millport, 26 Jul 1987, Gasparini 156 (IBE). ARIZONA. Pinal Co.: San Tan Village, near Sacaton, 29 Sep 1925, Peebles et al. 160 (ARIZ). New Jersey. Copper Point, 6 Nov 1932, Whitte s.n. (ARIZ). ARKANSAS. Benton Co.: Butler Creek bottoms, Sulphur Springs, $920 \mathrm{~m}, 2$ Sep 1966, Demaree 54209 (OKL, SMU, WIS). Crittenden Co.: W Memphis, 70 m, 16 Sep 1969, Demaree 61082 (IBE, SMU). Lincoln Co.: Gould, 32 m, Demaree 70227 (IBE). Montgomery Co.: top of Cristal Mountain, 580 m, 24 Nov 1965, Demaree 53340 (SMU, WIS). Nevada Co.: Prescott, 300 m, 15 Aug 1970, Demaree 62606 (DS, SMU). Pulaski Co.: Little Rock, 100 m, 20 Oct 1965, Demaree 52919 (OKL, SMU). Saline Co.: Benton, 90 m, 19 Sep 1965, Demaree 52912 (MSC, OKL, SMU, WIS). CALIFORNIA. Los Angeles Co.: Bryant Ranch, 13 Sep 1932, Wolf 5215 (RSA). Riverside Co.: ranch near Tamecula, 27 Sep 1940, Stubblefield 402998 (RSA). San Francisco Co.: San Francisco, Embarcadero at Montgomery Street, 22 Sep 1957, Howell s.n. (RSA, CAS, DAV). San Francisco, Fort Point, 29 Sep 1974, Norris 256346 (RSA). Santa Barbara Co.: Santa Barbara, 7 Sep 1957, 2 Oct 1957, Pollard s.n. (CAS, SMU).

Ventura Co.: Ventura River's bed near Casitas Spring, 24 Sep 1965, Pollard s.n. (CAS). Horn Canyon Creek near Ojai Avenue, 2 Aug 1960, Pollard s.n. (DAV). CONNECTICUT. Southington, 16 Sep 1904, Andrews s.n. (BH). FLORIDA. Alachua Co.: Gainesville, E side of SW $17^{\text {th }}$ Street, 20 Jul 1970, Perkins 663 (FLAS). W of Gainesville, ca. 1/2 mi W of I-75 on N side of FL 26, 12 Jul 1990, Gilliand 11 (FLAS, NA). Broward Co.: 2 mi W of Coral Springs, 21 Feb 1970, McCart 11305 (FLAS). Lee Co.: Western Sanibel Island, 6 Dec 1972, Brumbach 8126 (FLAS). Indian River Co.: W of Wabasso Island, 7 Aug 1968, D'Arcy 2299 (FLAS). GEORGIA. Elbert Co.: W of Elberton, garden of Stinchcomb Church Road, 23 Aug 1977, Dunn 1243 (FLAS). Ogelthorpe Co.: Lexington, 29 Sep 1965, Demaree 53018 (WIS). Illinois. Champaign Co.: Urbana, 2 Oct 1947, Jones 17668 (MIN). Union Co.: Panther's Den, 7 Aug 1959, MacMahon 715 (MIN). Randolph Co.: Old Kaskaskia, Kaskaskia Island, 21 Oct 1959, Evers 63076 (MIN). Madison Co.: Collinsville, 9 Nov 1967, Demaree 57461 (SMU,WIS). Jackson Co.: $21 / 2$ mi of Carbondale, 19 Oct 1985, Handel s.n. (CM). River Forest, 8 Oct 1896, E.T Harper \& S.A. Harper s.n. (ISC, WIS). Iowa Johnson Co.: Oxford Twp., $80^{\circ} \mathrm{N}, 08^{\circ} \mathrm{W}, 24$ Sep 1975, Kantor 605 (IA). 10 mi N of Johnston 20 Aug 1952, Anderson s.n. (WIS). Linn Co.: Coggon, 15 Oct 1965, McWilliam 15123 (US). Muscatine Co.: near Fruitland, 25 Sep 1909, Shimk s.n. (IA). Pine Mills, 28 Aug 1892, Reppert s.n. (IA). INDIANA. Jackson Co.: near Carbondale, 19 Oct 1985, Handel s.n. (CM). Ripley Co.: along Laughery Creek, E of Friendship, 13 Oct 1934, Deam 55896 (MIN). Steuben Co.: E side of James Lake, 20 Sep 1914, Deam 15484 (MIN). Cloud Co.: Concordia, between 5 \& 6 Streets, 1 Sep 1940, Fraser 622 (KSC). Salem, 20 Jul 1930, Brooks 1445 (SMU). KANSAS. Riley Co.: Manhattan, H.A. Goff Farm, 23 Sep 1969, Goff s.n. (KSC). Saline Co.: Salina, 31 Aug 1930, Hancin 695 (KSC). 17 Aug 1931, Blake 11380 (MSC). Cambridge, 27 Sep 1896, Blankinship s.n. (ISC). MICHIGAN Lanawee Co.: Hidden Lake Gardens of Michigan State University, 15 Sep 1960, Freeman 18 (MSC). MISSISIPPI. Grenada Co.: 2.7 mi N of Gore Springs, 12 Aug 1986, Morris 2471 (IBE). Leflore Co.: 7.5 mi N of Green Wood, 27 Aug 1959, McDaniel 1276 (IBE). Jones Co.: 1 mi E of Laurel, 29 Sep 1978,Morgan 1279 (IBE). Madison Co.: NatchezTrace Parkwey, 22 Sep 1948,McDougall 1777 (US). Monroe Co.: vicinity of Aberdeen, 4 Sep 1994, MacDonald 7599 (IBE). Washington Co.: Just N Leland, 28 Aug 1990, Bryson 10271 (IBE). Missouri. Kansas City, 25 Sep 1913, Rose 15133 (US). Jackson Co.: 14 Oct 1943, Bush 316 (MIN). Jasper Co.: Webb City, 7 Oct 1949, Palmer 49851 (UMO). Lawrence Co.: Sycamore Hollow, 20 Sep 1950, Palmer 51143 (UMO). Lincoln Co.: N of Troy, 15 Sep 1952, Sauer 1616 (WIN). St. Louis Co.: Saint Louis, 20 Sep 1975, Boufford \& Muehlenbach 17995 (CM); s.I., 21 Aug 1949, Shinners 11568 (MIL, SMU, WIS). Nevada Clark Co.: 1.5 mi S of Moapa, 450 m, Niles 3100 (ARIZ). NORTH CAROLINA. Chemung Co.: Elmira, 21 Sep 194, Smith 2306 (BH). Granville Co.: Wilton, 2 Sep 1937, Godfrey 2150 (NA). Iredell Co.: 0.8 mi W-NW of Scotts, then 2.6 mi S, 24 Oct 1958, Ahles 51921 (FLAS). Orange Co.: Korstian Division, E of Route 1712,400 m, 22 Sep 1988, Palmer 1333 (DUKE). Wake Co.: 0.5 mi NW of Sandy Ridge or the intersection of NC 50 and County Road 1900, Wilbur 45364 (DUKE). Wilson Co.: State Road 1649, 3 mi S of Lucuma, 22 Oct 1991, Wilbur 60002 (DUKE). NEW YORK. Bronx Co.: New York, near the Botanical Garden, 21 Oct 1986, Nee 33270 (CM, WIS). Kings Co.: Long Island, 25 Sep 1955, Brooks 3977 (BH). Tompkins Co.: ca. 2 mi S of Ithaca, 22 Sep 1943, Schuster 8217 (DUKE). Ithaca, 1 Oct 1941, Thorne 213 (IA). Ithaca, 6 Oct 1926, Bailey s.n. (BH). 10 Sep 1917, Bailey s.n. (BH) 21 Aug 1916, Metcalf 6395 (BH). Ohio. Portage Co.: Kent, 20 Sep 1913, Hopkins s.n. (CM). Richland Co.: Mansfield, 12 Aug 1895, Wilkinson s.n. (BH). OKLAHOMA. Kay Co.: near Tonkawa, 4 Aug 1913, Stevens 1841 (US). Cleveland Co.: Little River bottoms, 25 Sep 1920, Jeffs 1309 (OKL). Muskogee Co.: s.I., 28 Aug 1927, Little Jr. $2711,2487,2197$ (OKL). Ottawa Co.: Ottawa, 29 Aug 1913, Stevens 2557 (MIN). PENNSYLVANIA. Allegheny Co.: 4 km N. of Tarentum, 2 Sep 1990, Zand 339 (BH, CM). Bearer Co.: 18.2 mi Wet Raccon St. Park., 9 Oct 1965, Farnsworth s.n. (CM). near Georgetown, along Ohio River shore, 1 Sep 1951, Henrici 15112 (CM). Bedford Co.: $1 / 2 \mathrm{mi} \mathrm{S}$ SE Hyndman, 300 m, 2 Sep 1940; Berkheimer 2212 (CM). Berks Co.: $1 / 2 \mathrm{mi} \mathrm{S}$ of Bethel, $110 \mathrm{~m}, 19$ Sep 1948, Berkheimer s.n. (IA). 2 mi NE of Kutztown, 6 Oct 1986, Nee 33266 (CM). Butler Co.: Petersville, 23 Aug 1922, Herbert \& Graham s.n. (CM). Centre Co.: Oak Hall, Mill Pond, 10 Sep 1939, Wahl 434 (BH). Delaware Co.: Upper Darby, 0.2 mi SE of intersection between Marshall Road and $69^{\text {th }}$ street Boulevard, 30 Sep 1941, Wheeler 603148 (RSA). Westmoreland Co.: Penn, South Huntington Township,
$40^{\circ} 14^{\prime} \mathrm{N}, 79^{\circ} 45^{\prime} \mathrm{W}, 270 \mathrm{~m}, 12$ Aug 1974, Utech 94-1959 (CM). TENNESSEE. Davidson Co.: s.f. unknown locality cultivated at Ames, Iowa, 1 Oct 1965, McWilliams 1826 (WIS). Lake Co.: Near Markham, 15 Aug 1947, Sharpet al. 6266 (WIS). Shelby Co.: Presidents Island, Memphis, 60 m, 25 Oct 1952, Demaree 33190 (GH). Washington Co.: Johnson City, 813 Forest Avenue, 15 Oct 1994, Churchill 94206 (MSC). TEXAS. Brazos Co.: College Hills Woodlands (cultivated), 9 Sep 1942, Reeves s.n. (SMU). Sunset Co.: 8 mi Tyler, 14 Oct 1944, Moore 917 (BH, GH). VIRGINIA. Bedford Co.: 15 Sep 1869, Curtiss s.n. (GH). Quantico, 20 Aug 1915, Tidestrom 7582 (NA). Campbell Co.: intersection of Waterlik and Leesville Rds., 26 Aug 1978, Ramsey \& Freer 26303 (SMU, WIS). Diggs Beach on St. Rte. 643, 8 Oct 1978, van Montfrans 2106 (FLAS). Giles Co.: New Port, 580 m, 14 Aug 1958,Iltis 19938 (WIS). Wisconsin. Richland Co.: 1 mi NE of Richland Center, 20 Aug 1983, Nee 43787 (MO). Rock Co.: near Edgerton, 5 Sep 1952, Sauer 1597 (WIS). WASHINGTON D.C. 10 Sep 1897, Steele s.n. (DUKE); s.l., 11 Aug 1949,Freeman 417 (NA).

MEXICO AND GREATER ANTILLES. BERMUDA. St. George Island: South Road, 31 Aug 1913, Collins 189 (GH);s.I., 10 Mar 1908, Brown 538 (GH). MEXICO. Chiapas: Mpio. Pokolum, Tenejapa 1600 m, Breedlove 6091 (DS); s.I. 22 Nov 1964, Breedlove 7423 (WIS). Chihuahua: Mpio. Batopilas, Barranca de Batopilas, $2100 \mathrm{~m}, 10$ Oct 1973, Bye 5391 (ECON). Nobogame, $28^{\circ} 30^{\prime} \mathrm{N}, 108^{\circ} 30^{\prime} \mathrm{W}, 1800 \mathrm{~m}, 10$ Sep 1987, Laferriere 545 (WIS). Hidalgo: San Bartolo, Tutotepec, 1000 m, 4 Nov 1973, Gimate 861 (ARIZ, UMO, CAS). Distr. Federal: Mexico City, campus of UNAM, 2300 m, 4 Sep 1986, Nee 32980 (CM, WIS). Jalisco: Guadalajara,Oct 1896, Palmer 626,629,630 (GH,US). 15 km W of Guadalajara, $20^{\circ} 43^{\prime} \mathrm{N}, 103^{\circ} 24^{\prime} \mathrm{W}$ $1700 \mathrm{~m}, 26$ Sep 1978, Iltis \& Lasseigne 625 (WIS). Volcan Colima, $19^{\circ} 39^{\prime} \mathrm{N}, 103^{\circ} 32^{\prime} \mathrm{W}, 1750-1800 \mathrm{~m}, 24$ Sep 1978, H.H. Ilis et al 559 (WIS). Michoacan: N of Mason Nuevo, 2300 m, 31 Jul 1977, Bennett et al. 721 (UMO). Distr. Ixtlan, Mpio. Comaltepec, S of Comaltepec, $17^{\circ} 33^{\prime} \mathrm{N}, 96^{\circ} 31^{\prime} \mathrm{W}, 2000 \mathrm{~m}, 8 \mathrm{Dec} 1987$, Lopez Lopez 5 (MO). Nuevo Leon: 35 mi of Monterrey, Hacienda Vista Hermosa, 700 m, 27 Jun 1939, White 1592 (ARIZ). Oaxaca: Nayarit, 11 Jul 1948, Sauer 28 (MO). Valley of Etla, Sep 1895, Aloarry 749 (GH). Puebla: Puebla, Rancho Pasadas, 2194 m, 25 Aug 1909,Nicolas 292 (CM).Veracruz: Distr.Papautla, Tajin, 3 Dec 1947, Gonzales 105 (BH). Mpio. Xalapa, Claviejo, Xalapa Botanical Garden, 19³0'30'N $96^{\circ} 56^{\prime} 30^{\prime \prime}$ W, 300 m, 18 Sep 1986, Nee 33066 (WIS, CM). Remundandero, Feb 1923, Purpus 8870 (GH). Mpio. Emiliano Zapata, Barranca de San Antonio, 590 m, Hernadez 62 (MO). between Veracruz and Villahermosa, km marker 180, 70 m , Croat 62122 (MO).Mpio. Coatepec, 3 km N of Coatepec, $19^{\circ} 29^{\prime} \mathrm{N}$ $96^{\circ} 57^{\prime}$ W, 1250 m, 22 Aug 1986, Nee 32852 (WIS). Rancheria Palmas Cuatas, Ignacio de la Llave, 6 m, 12 Aug 1966, Martinez 21739 (DAV). BAHAMAS. Crooked Island: Landrail Landing, 6 Jun 1977, Corell \& Proctor 48773 (US). CUBA: Valley of San Angustina, 21 Mar 1903, Britton et al. 512 (CM). GUATEMALA. Dep. Alta Verapaz: s.f. Coban cultivated at Davis, California 29-31 Oct 1948, Sauer 1309 (WIS). Dep. Juatipa: 1.2 km N of el Progreso ( W side of the Road) to Jalapa, 1040-1060 m, 27, 30, 31 Dec 1975, Iltis G-14 (WIS). Dep. Santa Rosa: Santa Rosa, 930 m, Aug 1892, Heyde \& Lux 4062 (GH). NICARAGUA Dep. Esteli: Santa Cruz, $13^{\circ} 01$ N, $86^{\circ} 18^{\prime}$ W, 950-1000 m, 9 Nov 1980, Moreno 4561 (MO). Loma Ocotecalzado, $13^{\circ} 10^{\prime} \mathrm{N}, 86^{\circ} 18^{\prime} \mathrm{W}, 1260-1300 \mathrm{~m}$, Stevens et al 15589 (MO). COSTA RICA. Prov.Cartago: Cartago, 1400 m, Nov 1887, Cooper 5908 (GH, US). Prov. San Jose: San Jose, 1100 m, Jan 1896, Tanduz 9856 (GH). PANAMA. Chiriqui: vicinity of Boquete, 1000-1250 m, 12-13 Dec 1966, Lewis et al 594 (GH, NA, UC). Bambito, 1400 m, 12 Mar 1974, Tayson 7240 (US).

SOUTH AMERICA. COLOMBIA. Cauca: Cordillera Central, River Palo, between Tacueyo and La Tolda, 1780-1900 m, 14 Dec 1944, Cuatrecasas 19472 (GH). BRASIL: Bello Horizonte, 1000 m, 5 Mar 1945, William \& Assis 6461 (GH). Goias: Corumba de Goias, $16^{\circ} \mathrm{S}, 49^{\circ} \mathrm{W}, 1000 \mathrm{~m}, 3$ Dec 1965, Irwin et al 10991 (RB). Parana: Parque Nacional de Iguacu, Picado do Benjamin, 400 m, 26 May 1949, Duarte \& Pereira 1911 (RB). Rio Grande do Sul: Minas, 16 Apr 1935, Hoffman 6 (RB). BOLIVIA. Yungas. 1890, Bang 231 (GH). Hacienda Simaco above the road to Tipuani, 1400 m, Jan 1920, Buchtien 5401 (GH).

3b. Amaranthus hybridus subsp. quitensis (Kunth) Costea \& Carretero, comb.
nov. Basionym: Amaranthus quitensis Kunth, Humb., Bonpl. \& Kunth, Nov. Gen. Sp. 2., folio: 156; ed. 4:194. 1817. A. retroflexus L. subsp. quitensis (Kunth) O. Bolos \& Vigo, Butll. Inst.

Catalana Hist. 38:89. 1974. A. hybridus L. var. quitensis (Kunth) Covas, Darwiniana 5:329-368. 1941. TYPE: ECUADOR: "Crescit in ripa fluvii Guallabambae, alt 1030 hex," (Regno Quitensi), 6, 1802, Humboldt \& Bonpland 3082 (Holotype: P?).
Amaranthus caudatus sensu Greuter et al., Med-Checkl. 1:46. 1984. p.p., non L. s. str.
Cotyledons lanceolate, $12 \times 2-2.5 \mathrm{~mm}$, with acute apex. Pollen grains $25-30 \mu \mathrm{~m}$ with $28-35$ pores of $1.2-1.4 \mu \mathrm{~m}$ in diameter. The pollen differs to subsp hybridus by the tectum with high density of spinules. (Fig. 2, F). 2n=32.

We share a different view from Coons $(1975,1978)$ over the boundaries of this taxon. The tepals can be variable, erect to recurved as in other species (for example Amaranthus retroflexus). More important are the length and shape of tepals. Therefore the type of this taxon is indeed Humboldt \& Bonpland 3082 deposited in Paris (P).

The length of bracteoles is variable in subsp. quitensis too. Typically the bracteoles are 1.5-2 times longer than the tepals. The plants from Galapagos Islands have shorter bracts, 1-1.2 times longer than the tepals and also stand apart in that their flowers have tepals and bracteoles with very large, ramified, green mid-veins with very narrow membranous margins. In the present account we do not include A. hybridus var. sangorache (Coons 1975, 1978) within A. hybridus subsp. quitensis more research being necessary in order to clarify the status of this taxon.

Distribution and ecology.-A native riverbank pioneer in tropical South America, where it is a noxious weed, this plant is more dependent on a warm climate than subsp. hybridus. Even though it was recorded in Europe since the 19th century, as a casual in most countries, it is naturalised only in the Azores and Balearic Islands (Akeroyd 1993). It has also been collected in Australia.

Representative specimens examined: SOUTH AMERICA. ECUADOR. Charles Island: Black Beach, 19 May 1932, Howell 9381 (CAS). Isabela Island: Tagus Cove, Jun 1899, Snodgrass \& Heller 219 (GH).
Santa Cruz: along "Old Trail" from Academy Bay toward Bella Vista, 5-100 m, 24 Jan 1964, Wiggins 18334A (CAS). Bella Vista, 200 m, 27 Jan 1967, Fosberg 44851 (RSA). Academy Bay, Apr 1953, Bowman 46110 (CAS). El Chato, 31 Jul 1966, Colinvaux s.n. (CAS).PERU.Dep. Cajamarca: Valley of Rio Chamaya, 36 km W of Pucara, $5^{\circ} 55^{\prime} \mathrm{S}, 79^{\circ} 19^{\prime} \mathrm{W}, 1100 \mathrm{~m}, 18$ Apr 1984, Croat 58375 (CAS). Dep. Cusco: Prov. Urubamba, $1 / 2 \mathrm{mi}$ E of Urubamba, 2800 m , Ittis \& Ugent 1160 (CAS). Dep. Piura: 37,3 km of Pucara, $5^{\circ} 47^{\prime} \mathrm{S}, 79^{\circ} 27 \mathrm{~W}, 1550 \mathrm{~m}$, Croat 58392 (CAS). BRASIL. Estado do Rio Grande do Sul: Serra Geral, 17 Mar 1983, Silveira \& Frosi 544 (RB). BOLIVIA. Andres Ibanez: 12 km E of center of Santa Cruz, $17^{\circ} 46^{\prime}$ to $47^{\prime}, 63^{\circ} 04^{\prime} \mathrm{W}, 375 \mathrm{~m}, 4$ Feb 1987, Nee 33988 (CM).W side of Santa Cruz, $17^{\circ} 47^{\prime} \mathrm{S}, 63^{\circ} 40^{\prime} \mathrm{W}, 420 \mathrm{~m}, 14$ Jan 1987, Nee 35481 (CM). 15 km of Cotoca, $17^{\circ} 42^{\prime} \mathrm{S}, 62^{\circ} 53^{\prime} \mathrm{W}, 325 \mathrm{~m}, 28$ Jan 1989, Nee 37776 (WIS).
Santa Cruz: Prov. Caballero: 2 km NW of Rio San Isidro bridge in San Isidro, along to highway to Comarapa, $18^{\circ} 02^{\prime} \mathrm{S}, 64^{\circ} 27^{\prime}$ W, 1575 m, 29 Dec 1995, Nee 46591 (ADA). Angostura, 550 m, 25 Jun 1966 Steinbach s.n. (RSA). ca. 21 km SE of Palmar del Oratorio, $18^{\circ} 02^{\prime} \mathrm{S}, 63^{\circ} 01^{\prime} \mathrm{W}, 365 \mathrm{~m}, 22$ Jan 1989, Nee 37648 (WIS). Ichilo, Buena Vista, $17^{\circ} 27^{\prime}$ S, $63^{\circ} 40^{\prime}$ W, $370 \mathrm{~m}, 2$ Aug 1987, Nee 33510 (CM). PARAGUAY.
Guaira:Tororo, Camino a Polilla, $25^{\circ} 55^{\prime} \mathrm{S}, 55^{\circ} 15^{\prime} \mathrm{W}$, 10 Dec 1988, Degen 1035 (MO). Centro Forestier, Pta. Stroessner - Alta Parana 250 m, 24 May 1982, Stuts 310 (MO). URUGUAY. Dep. Montevideo: Pocitos, Mar 1924, Herter 68154 (MSC, WIS). ARGENTINA. Prov. Buenos Aires: La Belgica, $17^{\circ} 34^{\prime}$ S, $63^{\circ} 13^{\prime}$ W, Nee 33475 (ISC). Hudson, 15 May 1945, Hunzinker 661 (A); s.I., 15 May 1945, Hunzinker 2260
(GH). Pergamino, 22 Mar 1929, Parodi 8910 (GH). Prov. Catamarca: Ancasti, Rio Chico, 28 Nov 1950, Brizuela 759 (CM). Dep. La Paz, El Bello, 3 Mar 1950, Brizuela 1211 (MICH, CAS). Prov. Chaco: Dep San Martin, La Leonor, 26-27 May 1988, Schinini 26222 (GH). Prov. Formosa: Dep. Pilcomayo, Ruta 86 al km 55, 9 Feb 1948, Morel 4594, 6542 (UMO). 3 km of Portenito, 6 Oct 1947, Morel 3857 (US). S of Laguna Primavera, 20 Dec 1949, Morel 9110 (CM). Prov. Misiones: Dep. San Pedro, Cataraguatay (Centro) 11 May 1949, Montes 1625 (CAS,WIS). Pasadas, 21 Jul 1945, Bertoni 1519 (A); s.l., 17 Nov 1907, Ekman 117, 118 (US, GH). Isla Pindoi, Jul 1945, Grovetto 3435 (CAS). Prov. Salta: El Potrero, 30 Mar 1950, Brizuela, 1099 (US). Dep. Boqueron, 68 km NE de Filadelfia, 10 Dec 1992, Krapovickas et Cristobal 44281 (MO). Dep. Candelaria, El Datil, 7 Feb 1949, Montenegro 349 (CAS). Dep Rosario de la Frontera, La Junta, 690 m, 29 Jan 1935, Carbone 12700 (GH). Prov. Tucuman: La Ramada, 450 m, 2 Apr 1933, Deirano 9666 (GH). Dep Rio Chico, Escaba, 600 m, 5 Dec 1913, Onetti 1653 (GH). Dep Seales, Ia Florida 270 m, Jun 1913, Monetti 11659 (GH). CHILE: s.f. Angol, grown at Cornell University, Jul-Aug 1937, Murray 36023 (10) (BH).
4. Amaranthus hypochondriacus L., Sp. Pl. 991.1753. (Fig. 5). TYPE: "Habitat in Virginia"; LINN 1117/24.

Amaranthus chlorostachys Willd. var. erythrostachys (Moq.) Aellen, Hegi, Illustr. Fl. Mittel.-eur. ed. 2, 3(1-2):482. 1959. A. hybridus L. subsp. hybridus var. erythrostachys Moq., DC., Prodr 13(2):259. 1849. A. hybridus L. var. hypochondriacus (L.) Robinson, Rhodora 10:32. 1908. A. hybridus L. subsp. hypochondriacus (L.) Thell. proles erythrostachys (Moq.) Thell., Ascherson \& Graebner, Syn. Mitteleur. Fl. 5:241. 1914.
Amaranthusflavus L. Syst. Nat. ed. 10. 2:1269. 1759.
Amaranthus frumentaceus Buch. Hamilt. ex Roxb., Fl. Ind. 3:613. 1832.
Amaranthus anardana Buch. Hamilt. in Wall. ex Moq.-Tand., DC. Prodr. 13(2):256. 1849.
Amaranthus leucocarpus S. Wats., Proc. Amer. Acad. Arts. 10:347. 1875.
Amaranthus leucospermus S.Wats., Proc. Amer. Acad. Arts. 22:446. 1887.
Like A. cruentus, but inflorescence usually stiff, with thick branches. Cotyledons as in A. cruentus but larger, $18 \times 5 \mathrm{~mm}$. Bracteoles $3-5 \mathrm{~mm}$ long, about 1.5 mm longer (sometimes 2 times longer) than the tepals. Tepals 5 , one equal to or longer than the fruit, the others 4 shorter, lanceolate, with the mid-vein brownreddish. Fruit circumscissile, tapering gradually toward the stigma region, 1.52 mm long, about 2 times longer than wide, with the dehiscence line in the upper half. Stigma branches thick, spreading, about $1.6-1.8 \mathrm{~mm}$ long and 0.60.8 mm wide at the base. Type of pericarp surface variable: A to B. All the other morphological characteristics of the fruits and dark seeds correspond to those of A. powellii. The pale seeds are very much like those described for A.caudatus, differing in having the cells of the exotesta inconspicuous (because their anticlinal walls are inconspicuous) and the periclinal walls evidently wrinkled. Pollen grains of $18-23 \mu \mathrm{~m}$, with 32-45 pores of 1.3-1.5 $\mu \mathrm{m}$ in diameter. Density of granules medium. $2 \mathrm{n}=32,34$.

Distribution and ecology.-This species is originally from North America, where its closest wild relative A. powellii is common, though at the same time it is evidently related to the cultivated A.cruentus. Sauer (1993) suggests that it is probable that it is of hybrid origin from those two taxa. This relationship is also supported by some molecular studies (Transue et al. 1994; Kirkpatrik 1995; Chan


FIG. 5. Amaranthus hypochondriacus, from Lehmann, AMES 2155 (NA)
\& Sun 1997). Like A.cruentus, it is cultivated as an ornamental, for grain and as a potherb.
Representative specimens examined: AFRICA. KENYA. Nairobi Distr.: Nairobi, Ministry of Works Estate, W Bahati, 1678 m, 12 Feb 1969, Mwangangi 1331 (MO).

ASIA. PAKISTAN. Baltistatan: Skardu, 2150 m, 16 Aug 1936, Koelz 9627,2928 (NA). Swat Distr.: Fatehpur, 1270 m, 17 Oct 1975, Shahet al 690 (A). INDIA: s.f. unknown locality cultivated at Kutztown, Pennsylvania, 12 Sep 1984, Strudwick \& Reider RRC 1175 (MO). Sholur, 15 Mar 1963, Noble \# M (NA, WIS). Kasalhado, 14 Feb 1963, Noble \#j (NA, WIS). E Jakatala, Badaga, 1780 m, 14 Feb 1963, Noble \# k (WIS). Northern Thuneri, 1900 m, 27 Jul 1993, Noble s.n. (WIS); s.l., 30 Aug 1964, Sauer 3952, 3942 ( NA, WIS). Jammu and Kashmir: Srinagar, 1400 m, 20 Sep 1956, Polunin 56/819 (MO, NA, WIS).Tangmarg, 1900 m, 16 Aug 1956, Polunin 56/300 (MO,WIS). Sind Valley, Rezan, 2400 m, 31 Aug 1956, Polunin $56 /$ 617 (MO, WIS, NA). near Miragund, 1400 m, 15 Sep 1959, Polunin 56/804 (WIS). Upper Nilgiri Hills, KilKotagari, 1800 m, 18 Sep 1962, Noble \# e (WIS). Wangat Nullah at Khanan, 2000 m, Polunin 56/759 (MO, NA). Tamil Nadu: near Coonoor, 21 Jan 1963, Noble \# b (NA, WIS). Madras, Kurumba Villages, 1370 m, 18 Nov 1962, 16 Dec 1963, 20 Jan 1963, Noble s.n. (WIS). s.f. Kurumba, 6 Oct 1964, Sauer 39496 (MO, WIS, NA); s.l., 2 Nov 1964, Sauer 3950, $3954 b$ (WIS, NA, MO). Uttar Pradesh: s.f. Mussorie, collected by Lal (1961), cultivated in New York, Ithaca, Aug-Nov 1969, Sauer 2845 (BH, NA, WIS). NEPAL: s.f. Marku Valley, Sirsagarhi, 10 Nov 1950, cultivated, Sauer 1495D (A). SRI LANKA. Distr.North Central Province: Anurahdapura, 60-61 mi from Kandy on the road to Jaffna South Kagama, 24 Feb 1973, Townsend 73/117 (US). Central Province: Matale Distr., Sigiriya Wewa, 11 Mar 1973, Townsend 73/205 (US). CHINA. Prov. Heilongjiang: Ping Shan, $45^{\circ} 57^{\prime} \mathrm{N}, 127^{\circ} 23^{\prime} \mathrm{E}, 370 \mathrm{~m}, 2$ Sep 1993, NACPEC, HLJ-37 (NA). Border between Prov. Hopeh and Honan, Chicungshan, 400-900 m, 18 Jun 1917, Bailey s.n. (BH). s.f. Muping Sikong, 2500 m, 10 Nov 1950, Sauer 1489-E (GH). Szechwan: s.ff. Mowhsien, 2000 m, 10 Nov 1950, Sauer 1499-F, 1484-D (GH). Yunnan: Muli, Wachin, Schawan, 3000 m,"side of field," 1937, Yu 14481, 14482 (A). Ho-pei: Near Chou Cheng, 26 Sep 1948, Beach 238 (US).

EUROPE. NORWAY. Oslo: Oslo, s.f. Botanical Garden, University Norway, 3 Sep 1940, Gillett 40-5-2 (NA). SWEDEN. Stockholm: Stockholm.s.f. Botanical Garden of Stockholm, Grant 225 (WIS). ITALY. Friuli Venezia-Giulia: s.f.Udine, Botanical Garden of Instituto Tecnico Zanon, Grant 426 (NA). FRANCE. Doubs: Besancon, s.f. Botanical Garden of the University de la Ville, Grant 428 (NA). Loire-Atlantique: s.f. Botanical Garden Nates, unknown date, Grant 223,227,227b (NA). 231 (WIS). HOLLAND. NoordHolland: Amsterdam, s.f. Botanical Garden of Amsterdam, Grant 131 (WIS). GERMANY. Nordrhein Westfalen: Bonn, s.f. Botanical Garden, University Bonn, Grant 428 (NA). AUSTRIA. Burgenland: Pamhagen, Aug 1954, Patzak s.n. (DAV). RUSSIA. s.f. unknown locality grown in Ithaca, New York, 31 Jul 1936, Muenscher s.n. (BH). ROMANIA. Cluj Co.: s.f.Cluj, cultivated at Ithaca, New York, 19 Jul 1970, Dress 9943 (BH). Mehedinti Co.: Orsova, ruderal, 9 Jul 1966, Morariu s.n (BUCA). LITHUANIA. Neman: s.f. Kaunas, cultivated in Ottawa, Canada, 1939, Zinck 39-97-7 (BH). IRAN: s.f. unknown locality cultivated at Glenn Dale, Maryland, 11 Aug 1939, Cowgill 2355 (BH).

NORTH AMERICA. CANADA. ONTARIO: Ottawa, cultivated at Dominion Botanical Garden, 29 Aug 1939, Lawrence 682 (BH). UNITED STATES. CALIFORNIA. San Bernardino Co.: San Bernardino Valley, $300 \mathrm{~m}, 16$ Sep 1907, Parish 6472 (MIN). Yolo Co.: Davis, on the campus, 10 Aug 1978, Kellner s.n. (DAV). FLORIDA. Citrus Co.: Inverness, 3385 South Highlands, 20 Jul 1989, Johnston s.n. (FLAS). KANSAS. Washington Co.: SE corner of the County, 13 Oct 1938, Holman s.n. (KSC). MICHIGAN. Gratiot Co.: Alma, Sept 1935, Davis s.n. (BH). MINNESOTA. Dakota Co.: Inner Grove, ruderal, 14 Sep 1930, Jones 513 (MIN). MISSOURI. Jakson Co.: Independence, 2 Sep 1895, Mackenzie 21111 (MIN, ISC). NEBRASKA. Adams Co.: Hastings, 20 Oct 1934, Rose de Lima 300 (CM). NEW YORK. Onondaga Co.: Syracuse, SE corner of Onondaga Lake, 21 Aug 1916, Wiegand 6396 (MO, GH). Tompkins Co.: Ithaca, "weed in garden," 14 Aug 1919, Bailey s.n. (BH); s.l., ruderal, 24 Aug 1925 Muenscher s.n. (BH). Cinders, College of Agriculture, ruderal, 12 Sep 1923, Burnham 15065 (BH). PENNSYLVANIA. Dane Co.: Murphy's Creek, 22 Aug 1945, Hale s.n. (WIS). Erie Co.: 10 Aug 1894, Miller s.n.
(CM). Stoyestown, 20 Jul 1873, Patterson 6210 (CM). WISCONSIN. Rock Co.: Beloit, 9 Aug 1936, Anthony s.n. (WIS). Oneida Co.: Minoqua (ruderal), 24 Sep 1981, Harrington 36 (WIS).

MEXICO. Chihuahua: Rio Mayo, Guasaremos, 20 Sep 1935, Scott Gentry 1844 (NA). s.f. Rancho Tigre, 17 Oct 1948 Sauer 1193, 1396 (BH, NA, WIS). Colima: Colima, August 1897, Palmer 120 (DS). Distr. Federal: s.f. Mpio. Atlapulco, San Gregorio, 28 May 1948, Saver 1171 (MO, GH, NA, WIS); s.I., 31 Oct 1948, Sauer 1211 (GH, MO, NA, WIS); s.I., 31 Jan 1949, Sauer 1404 (MO, GH, NA, WIS). Guerrero: s.f. Chilapa, 20 Aug 1948 - 21 Jan 1949, Sauer 1162-E (MO, GH, NA, WIS). Pemex N of Chilpancingo, "ruderal," 20 Aug 1972, Dunn et al. 20477 (UMO). Jalisco: Tlajomulco, 25 Aug 1947, Sauer 1174 (BH, GH, MO, NA, WIS). Mexico: Temascaltepec de Gonzales, Timbres, 1660 m, 15 Oct 1932, Hinton 2137 (MO). Mpio. Michoacan: Zacapan, 25 Aug 1947, Saver 1170 (BH, NA). Zacapu, 25 Aug 1947, Sauer 1395 (DS, MO, NA, WIS). Opopeo, 30 Oct 1948, Sauer 1274 (BH). Oaxaca: Clavillones in Zimatlan area, 30 Oct 1948, Sauer 1266 (MO, NA, WIS). Puebla: San Jeronimo Teocuizmalco, 31 Oct 1948, Saver 1239 (NA, WIS). Sonora: Rio Mayo, cultivated, 20 Sep 1935, Scott Gentry 1843 (GH). Rio Mayo, Rancho el Moschite, 11 Oct 1979, Nabhan GN 975 A (GA). Tlaxaca: San Berabe Amaxac, 5 Oct 1949, Sauer 1535 (GH, MO, UC, NA, WIS). San Miquel del Milagro, 30 Oct 1949, Sauer, 1288, 1293, 1277, 1139 (GH, MO, NA, WIS). Veracruz: between Tequila and Orizaba, $15^{\circ} 45^{\prime} \mathrm{N}, 97^{\circ} 5^{\prime} \mathrm{W}, 1600 \mathrm{~m}$, Jan 1984, B. Benz \& K. Benz 980 (WIS).
5. Amaranthus powellii S.Wats., Proc. Amer. Acad. Arts. 10:347. 1875. Type: Described from a plant cultivated at Harvard University "from seeds brought from Arizona by Col Powell," Powell s.n. (holotype: US 16163; ISOTYPE: MO).

Erect annual 0.5-1.5(-2) m, with stem glabrous to puberulent mostly in the inflorescence region, with trichomes multicellular and uniseriate. Cotyledons narrow-elliptic, $10-12 \times 3 \mathrm{~mm}$, with acute to rounded apex and acute to cuneate base; petiole about $5-6 \mathrm{~mm}$ long. Leaves, broadly-elliptic to rhombic or lanceolate, $3-8 \times 2-6 \mathrm{~cm}$. Bracteoles rigid, heavy, 4.5-6(-8) mm long, about 2-$3(-4)$ times longer than the tepals. Tepals 3-5, evidently unequal; one tepal is $2.2-3 \mathrm{~mm}$ long, the others $1.2-1.6 \mathrm{~mm}$ long, linear-lanceolate to elliptic, with the mid-veins inconspicuous (only in the longest tepal may be partially visible). The longer (outer) tepal surpassing the fruit, the shorter (inner) tepals shorter than (or as long as) the fruit. Fruit dehiscent or indehiscent, elliptical to obovoidal, 1.5-2 times longer than wide, when dehiscent with the dehiscence line in the upper half, gradually narrowed toward the stigma region, the apex of the fruit truncated. Stigma branches thick, spreading from the base, 1.9-2.2 mm long and 0.08-0.1 mm thick at the base. Seeds lenticular, differentiated into central zone and marginal zones. Colour black to dark brown, uniform. Pollen grains $18-23 \mu \mathrm{~m}$ with $30-45$ pores of $1.1-1.3 \mu \mathrm{~m}$ in diameter. Density of granules low to medium.

Sauer (1967) and afterward other authors (Jalas \& Suominen 1980; Carretero 1985, 1990; Akeroyd 1993 etc.) considered the "European" taxon A. bouchonii, to be conspecific with A powellii on the basis of their similarity. The study of isozymes (Wilkin 1992) failed to establish satisfactorily the distinctness of these two taxa, but the author maintained $A$. bouchonii at the specific level. The same option was followed by Cacciato (1982), Hügin (1986, 1987), Kerguélen (1993), Stace (1991, 1997).

Studying European plants we found the indehiscent character of the fruit
to be constant. For example, European plants of A. bouchonii cultivated for eight years in the vicinity of A. powellii, A. hybridus and A. retroflexus, in the Botanical Garden of the University of Agronomical Sciences Bucharest, maintained their character. Greizerstein and Poggio (1992); Greizerstein et al. 1997) found differencies in chromosome number, chromosomal asymmetry and total DNA that supports $A$. bouchonii as an independent taxon. There is also a tendency toward ecological separation of the two variants in Europe: A. bouchonii populations occur primarily along riverbanks as pioneers, while $A$. powellii is a ruderal or segetal weed.

Based on our observations, in North America, plants with indehiscent fruits are more variable than in Europe. Some of them could be easily associated with A. powellii but others with $A$. hybridus. In both situations the same plant may bear only indehiscent fruit (especially A. powellii) or a mixture of circumscissile, iregularly dehiscent and indehiscent fruits (especially A. hybridus-like plants). Sometimes the dehiscence line is partially visible but the fruit does not open. The phenomenon occurs naturally. It is possible that the process of evolution of this taxon is taking place simultaneously in America and Europe, and that in Europe the varieties with indehiscent fruits have acquired more stability and consistency. It is also probable that the European A. bouchonii forms have reached America.

After close morphological and anatomical examination we found some new characters that, together with the previous data, suggest the subspecies rank for the plants with indehiscent fruit.

1. Inflorescence stiff and erect, $\pm$ unbranched or with a few widely spaced, long branches. Fruit circumcissile, 2 times longer than wide, irregularly wrinkled above the dehiscence line, with the pericarp surface type A. Seeds with an indistinct furrow extending $1 / 3$ to midway through the seeds, with the marginal zone almost smooth $\qquad$ A. powellii subsp. powellii (Figs. 1A; 2 A, C;6)
2. Inflorescence often not strictly erect, more lax, with many lateral branches. Fruit indehiscent or irregularly dehiscent, 1.5 times longer than wide $\pm$ smooth with the type of pericarp surface variable: B to C. Seeds with a concavity above the hilum and the radicle, with the marginal zone evidently sculptured $\qquad$ A. powellii subsp. bouchonii (Figs. 1 E, F; 2 B;7)

## 5a. Amaranthus powellii subsp. powellii (Fig. 6).

Amaranthus chlorostachys Willd. var. pseudo-retroflexus Thell., Vierteljahrssch. Naturf. Ges. Zurich 52:443. 1907. Amaranthus hybridus L. subsp. hypochondriacus (L.) Thell. var. chlorostachys (Willd.) Thell. f. pseudo-retroflexus Thell., Ascherson \& Graebner, Syn. Mitteleur. Fl. 5:239. 1914. Amaranthus chlorostachys Willd. var. (subsp.) powellii (S. Wats.) Priszter, Ann. Sect. Hort. Vit. Budapest, 2 (2):144.1953. Amaranthus hybridus L. subsp. hybridus var. pseudoretroflexus (Thell.) Carretero, Collect. Bot. 11(4):125. 1979.
Amaranthus chlorostachys sensu Hayek, Prodr. Fl. Penins. Balcan. 1:160. 1927.; Davis, Fl. Turkey 2:341. 967; Cacciato, Fl. Ital. 1:179. 1982.
Amaranthus hybridus" sensu Aellen in Tutin \& al. (eds.), Fl. Eur, ed 1, 1:109 (1964); Fl. Palaest. 1:181. 1966.


FIG. 6. Amaranthus powellii subsp. powellii, from the type (Powell s.n., US 16163).

Amaranthus hybridus subsp. hybridus sensu Townsend, p.p., non L. s. str., Fl. Zambesiaca 9(1):49. 1988.

Amaranthus hypochondriacus sensu Greuter et al., Med-Checklist l:47. 1984. p.p., non L. s. str.
Amaranthus hypochondriacus var. chlorostachys sensu Morariu, Fl. R.P.R. 1:586. 1952.
Inflorescence stiff, erect, $\pm$ unbranched or with a few widely spaced, long branches; the terminal branches are usually much longer than the lateral ones. Bracteoles usually 2-3 times longer than the tepals. Fruit 2 times longer than wide, coarsely wrinkled above the dehiscence line. Pericarp surface type A (Fig. 1 A). Seeds elliptic to obovate, $1.25-1.3 \times 1-1.1 \mathrm{~mm}$, the marginal zone almost smooth. Cells of the exotesta with inconspicuous anticlinal and almost smooth, plane periclinal walls (Fig. 2, A, C); border of the seed acute. $2 \mathrm{n}=32,34$.

Distribution end ecololgy.-Worldwide weed, native to North and South America. In Europe it is a very frequent ruderal and segetal weed frequently mistakenly called "A chlorostachys," "A.hybridus" or "A hypochondriacus."
Representative specimens examined: AFRICA. ETHIOPIA. Shewa: Addis Ababa, near University College, 2300 m, 13 Dec 1965, Wilde Duyfies 9235 (MO). Alemaya, College of Agriculture, $2050 \mathrm{~m}, 9$ Apr 1968, Westphal \& Westphal Stevels s.n. (MO). UGANDA: Muzingura-Kashaarara, $00^{\circ} 20^{\prime}$ S, $30^{\circ} 26^{\prime}$ E, $1900 \mathrm{~m}, 16$ Dec 1987, Rwaburindore 2550 (MO). TANZANIA. Iringa: Mufindi, $8^{\circ} 31^{\prime} \mathrm{S}, 35^{\circ} 10^{\prime} \mathrm{E}, 30 \mathrm{May}$ 1989, Kayombo 642 (MO).

ASIA. PAKISTAN. Kurram Valley Distr.: Makai to Parachinar, 1700 m, 15 Oct 1975, Dar \& al. 77 (A). INDIA. Jammu and Kashmir: Upper Nilgiri Hills, 1930 m, 23 Jun 1963, Noble s.n. (WIS).

AUSTRALIA AND OCEANIA. AUSTRALIA. New South Wales, 15 Mar 1970, Michael M6 (WIS). NEW ZEALAND. Waitemata Co.: Marangi Bay, $36^{\circ} 44^{\prime}$ S, $174^{\circ}{ }^{\circ} 5^{\prime}$ E, 30 Mar 1974, Bangerter 5157 (NA).

NORTH AMERICA. CANADA. Lambton Co.: Forest, 2 Oct 1963, Geiser 3374 F (WIS). UNITED STATES. ARIZONA. Cochise Co.: Chiricahua Mountains, W side of mountain, on road to Chiricahua National Monument, 2150 m, 14 Oct 1943, Kearney \& Peebles 15119 (CAS). Coconino Co.: Homestead,Flagstaff, $2100 \mathrm{~m}, 15$ Aug 1935, Whiting 756/1471 (ARIZ). CALIFORNIA. Alpine Co.: Markleeville, 1800 m, 10 Aug 1964, Howell 40910 (CAS). Inyo Co.: White Mountains, Antelope Springs, 1800 m, 22 Aug 1985, Morefield 3110 (ARIZ). Lassen Co.: Sierra Nevada, Susanville, 1400 m, 8, 9 Jul 1974, Howell 50500 (CAS). Monterey Co.: King City, 5 Aug 1963, Howell 39616 (CAS). 7 Aug 1963, Howell 40067 (CAS). San Joaquin Co.: 5 mi W of Stockton, 14 Aug 1953,Sauer 1642 (WIS). Santa Barbara Co.: San Antonio Road near Hollister Ave., 19 Aug 1957, Pollard s.n. (CAS). Santa Clara Co.: San Francisco Creek, 29 Jul 1973, Wiggins 22055 (DS). Sonoma Co.: near Guerneville, 3 Sep 1951, Rubtzoff 734 (CAS).
Ventura Co.: Ojai Valley, Lama Drive, 8 Nov. 1967, Pollard s.n. (CAS, MIN). Ojai, Ojai Avenue, between Gorham Road and San Antonio Creek crossing, 16 Oct 1966, Pollard s.n. (CAS). along Front Street, 5 Oct 1960, Pollard s.n. (CAS). Mirror Lake, 25 Jul 1959, Pollard s.n. (CAS). Southern Pacific Road, near San Juan Barranca crossing, 20 Sep 1960, Pollard s.n. (CAS). Ortonville, 19 Oct 1962, Pollard s.n. (CAS). Yolo Co.: Merrit Island, near junction 140 and 142, 3.5 mi S Clarksburg, 18 Aug 1969, Quick $69-20$ (CAS). McKinley Co.: Zuni reservation, 13 Aug 1978, Nabhan 1037 (ARIZ). COLORADO. Adams Co.: Bennett, Kiowa Creek at route 36 bridge, 2 Sep 1974, Churchill s.n. (MSC). Mineral Co.: Don Juan Mountains, 5 mi bellow the summit Wolf Creek Pass, $2600 \mathrm{~m}, 28$ Jul 1928, Wolf 3074 (CAS, DS, BH). IDAHO. Blaine Co.: Hailey, 23 Aug 1909, Woods \& Tidestrom 2814 (US). Spencer, 26 Jun 1916, Rust 420 (CAS). Nez Perces Co.: Forest, 17 Jul 1896, 1100 m, A.A. Heller \& E. G. Heller 3428 (US). IOWA. Palo Alto Co.: Lost Island Lake, 17 Jul 1934,Ada Hayden 4006 (IA).MASSACHUSETTS. Hampshire Co.: Haydenville, 3 Sep 1975, Ahles 81290 (UMO, CM, IA). Bristol Co.: Dighton, 5 Oct 1956, Seymour 17042 (WIS). Worcester Co.: Lancaster, 12 Sep 1943, Seymour 6006 (WIS). Leicester, 7 Aug 1944, Gates s.n. (WIS). MICHIGAN. Grawford Co.: 1 mi N of Seven Mile Road and 4 mi W of Beaver Creek Road, 14 Sep. 1992,

Chittenden \& Peil 1108 (MSC). Allegon Co.: Holland, Hope College, 16 Sep 1976, Gillis 13485 (MSC).
Shiawassee Co.: 12458 Warner Rd., Laingsburg, 17 Aug 1984, Harwood 285445 (MSC). Mecosta Co.: along Michigan Northern Railroad track, 50 m W of center of village Stanwood, 29 Aug 1984, Rabeler 832 (DUKE,MSC). MINNESOTA. Freeborn Co.: Albert Lea, 16 Sep 1979, Ownbey 6495 (MIN). Heunepin Co.: Minneapolis, N end of University of Minnesota campus, 17 Sep 1970, Ownbey 4398 (MIN). Mower Co.: Brownsdale, 26 Aug 1981, Smith 5576 (MIN). Washington Co.: along the street Criox River, 26 Sep 1988, Smith 15117 (MIN). MISSOURI. Jasper Co.: near Joplin, 17 Aug 1920, Palmer 18754 (UMO). St. Louis, 7 Apr. 1958, Muehlenbach 1435 (UMO); s.I., 26 Jun 1971, Muechlenbach 3587 (MO, NA). NEVADA. S of Carlin, 26 Aug 1984, Williams \& Tiehm s.n. (CAS). Lander Co.: Trout Creek, 16 Aug 1937, Goodner \& Henning 67842 (DUKE). Washoe Co.: N of Sparks, near Wild Creek Golf Course, 1100 m, 14 Sep 1984, Williams s.n. (CAS). NEW MEXICO. Dona Ana Co.: Organ Mountains, 1400 m, 23 Sep 1906, Wooton \& Standley s.n. (US). Grant Co.: Fort Bayard, 28 Aug 1905, Blumer 42 (GH). Valencia Co.: El Morro National Monument, 4 Aug 1939, Vogt 20 (ARIZ). NEW YORK. Chemung Co.: Elmira, 20 Sep 1941, Smith 2303, 2304 (BH). Madison Co.: Oneida Lake, 6 Sep 1939, Allen 20005 (BH). Tompkins Co.: South Hill, Ithaca, 23 Aug 1933, Allen 18316 (BH). OREGON. Benton Co.: (without location) 1908, Gilkey s.n. (US). Polk Co.: along Hwy. 99 W, N of Hoffman Road, 16 Jul 1982, Hasse 2513 (ARIZ). PENNSYLVANIA. Bedford Co.: Coleraine township school, Route \#326, 3 Sep 1972, Duppstadt s.n. (MIN). near Cessna, 30 Aug 1941, Berkheimer 2934-B (CM). Berks Co.: 2 mi NE of Kutztown, 6 Oct 1986, Nee 33265 (CM). $1 / 2$ mi NE of Trexler, 18 Aug 1953, Schaeffer 44911 (US). Lawrence Co.: 0.25 mi SE of New Bedford along Marr Road. 8 Sep 1990, Bonnie \& Isaac 354389 (CM). RHODE ISLAND. New Port Co.: Block Island, Old Harbor, 19 Aug 1913, Fernald \& Long 9463 (GH). TEXAS. Brewster Co.: Chisos Mts., 4 Aug 1931, Mueller 7986 (US). UTAH. Iron Co.: Cedar City, 1900 m, 15 Sep 1968, Howell \& True 45349 (CAS). Salt Lake Co.: Salt Lake City, 28 Aug 1939, W.C. Muenscher \& M.V. Muenscher, 15913 (BH). WISCONSIN. Columbia Co.: 1 mi W at Hwy 51, 22 and 60 intersection, 22 Sep 1964, Weis 30 (WIS). 1 mi SW of Columbus, 10 Sep 1956, Iltis \& Koeppen 8174 (WIS). Dane Co.: Madison, Oct 1949, Bergseng s.n. (WIS). Green Co.: roadside in Juola, 29 Sep 1957, Fell 57-1400 (WIS). Jefferson Co.: 1.5 mi NE of Fort Atkinson, 6 Sep 1981, Nee 21934 (WIS). Milwaukee Co.: Milwaukee, Lake Park, 15 Aug 1939, 20 Aug 1939, Shinners 983, 985 (MIL, WIS). Lincoln Co.: Near Round Lake, 22 Aug 1955, Seymour 16239 (WIS). Ozaukee Co.: Grafton, 8 Sep 1973, Strenger 37 (WIS). Portage Co.: 9 mi W of Plover River, 31 Jul 1964, Mauritz 867 (WIS). WYOMING. Goshen Co.: Southern Powder River Basin/SE Plains: Goshen Hole, Bump Sullivan Reservoir, ca. 4 mi S of Yoder, 1300 m, 28 Aug 1994, Nelson 34530 (UTEP). Laramie Co.: near Hillsdale, 1800 m, 14 Aug 1959, Porter \& Porter 8019 (DS, CAS). Yakima Co.: Washington, Naches Heights, 31 Aug 1937, W.C. Muenscher \& M.V. Muenscher 11292 (BH).

MEXICO. Baja California: Rio Santo Domingo, 4 mi above Mission, 12 Sep 1930, Wiggins \& Demaree 4789 (ARIZ). Santa Catarina, 1200 m, Broder 363 (DS). Chihuahua: Mojarachic, 25 Aug 1938, Knobloch 5513 (MSC). Temosachi, Nabogame, $28^{\circ} 00^{\prime} \mathrm{N}, 108^{\circ} 30^{\prime} \mathrm{W}, 1800 \mathrm{~m}$, Laferriere 546 (ARIZ). Hidalgo: near Tolcayuca 2350, 23 Aug 1970, Baron 55 (CAS, UMO). Zempoala 2450 m, 28 Sep 1975, Ventura 339 (UMO). Michoacan: 10 mi of Hidalgo, 7 Jul 1947, Sauer 1112 (MO). $1 / 3 \mathrm{mi}$ N on road to La Barca, $19^{\circ} 58^{\prime}$ N, $102^{\circ} 16^{\prime}$ W, 29 Jul 1960, Saver 491 (WIS). Morelos: Jiutepec, Jul 1965, Alcocer 8 (ISC). Sonora: Las Tierritas de El Temblor, Sierra de El Tigre, 18-24 Aug 1940, White 3393 (DS).

SOUTH AMERICA. PERU. Dep. Arequipa: Prov. Caraveli, 20 Km N of Puerto Chala, 15 Jan 1963, H.H Iltis, C.M. Iltis, D. Ugent \& V. Ugent 1578 (WIS). Dep. Lima: Prov. Huarochiri, Surco, 2000 m, 24 Apr 1940, Asplund 11025 (US). BOLIVIA. Dep. Chuquisaca: Prov. Oropeza, Villa Maria, 12 Apr 1963, D. Ugent \& Carderas 4948 (WIS). CHILE. Prov. Cautin: Temuco, 110 m, 2 Mar 1935, Montero 2303 (GH).

5b. Amaranthus powellii subsp. bouchonii (Thell.) Costea \& Carretero, comb. nov.
(Fig. 7). BASIONYM: Amaranthus bouchonii Thell. in Monde Pl. 27 (160):4. 1926. A. hybridus L. subsp. bouchonii (Thell.) O. Bolos \& Vigo in Butl. Inst. Catalana Hist. Nat. 38:89. 1974. A. hybridus L. var. bouchonii (Thell.) Lambinon. Candollea, 52:239-279. 1997. Type: Bordeaux, Allee du Boutant, Chemin remblaye avec des balayures du port, $25 \operatorname{Sep} 1925$, A. Bouchon (holotype: ?)


Fig.7.Amaranthus powellii subsp. bouchonii, from Carraway and Vertes 8 (UTEP).

Inflorescence of ten not strictly erect, more lax with many lateral branches. Bracteoles shorter and thinner compared to subsp. powellii,1.8-2.3 times longer than the tepals. Fruit indehiscent, about 1.5 times longer than wide, with the pericarp $\pm$ smooth. Pericarp surface type B to C (Fig. 1, E, F). Seeds usually broadovate to round (rare obovate), $0.9 \times 1-1.2 \mathrm{~mm}$, with the marginal zone sculptured and the margin of the seed usually rounded (Fig. 2 D). Cells of exotesta with prominent anticlinal walls, polygonal, $25-30 \mu \mathrm{~m}$ length; periclinal walls plane, finely sculptured. The origin unknown with certitude but relationship with A. powellii subsp. powellii undeniable. $2 \mathrm{n}=32$.

Typical specimens examined:EUROPE. NETHERLANDS. Prov. Noord-Holland: Beverwijk, 23 Aug 1983, Akkerman s.n. (UTEP). FRANCE. Puy-de Dome: Clermont-Ferand, unknown author, Sep 1960 (MSC, SMU). Gironde: Bordeaux, Jul 1960, Aellen s.n.(A). SWITZERLAND. Haut-Rhin: Sundhoffen, 9 Sep 1962, Aellen s.n. (A). ITALY. Lombardy: Comosee, 23 Aug 1984, Neuffco 386 (UTEP).

NORTH AMERICA. UNITED STATES. CALIFORNIA Los Angeles Co.: Arcadia, Winie Way and Santa Anita, 24 May 1962, Schmid s.n. (DAV). Fresno Co.: Huntington Lake, Big Creek, 1400 m, 23Aug 1951, Pollard s.n. (CAS). Plumas Co.: Belden, $660 \mathrm{~m}, 21 \mathrm{Sep} 1959$, Howell 43244 (CAS). Riverside Co.: Riverside, Sanders 20048 (UCR,UTEP). Ventura Co.: Santa Monica Mountains, 1 mi SE of Camarillor, 200 m, 19 Sep 1958, Raven \& Thompson 13726 (CAS). OREGON. Benton Co.: 4.5 mi N of Corvalis on Highland Drive, 6 Aug 1979, Carraway \& Verts 11200 (UTEP). Colorado Lake Road, 4 Oct 1959, Johnson 93 (IA). Hood River Co.: 10 Sep 1924, Henderson 300 (MO). MONTANA. Lake Co.: in the vicinity of Montana Biological Station, Yellow Bay, E shore of Flathead Lake, 850 m, 5 Aug 1965, Thomas s.n. (DS). PENNSYLVANIA. Bucks Co.: West Bristol, along Pond Street, 20 Jul 1950, Long 71768 (CM). Thurston Co.: 5 mi W of Olimpia, 15 Aug 1936, Meyer 786 (GH). WASHINGTON. Whatcom Co.: Lynden, 21 Aug 1939, Munscher 10558 (BH). Ten Mile, 31 Aug 1943, Munscher 16104 (BH). King Co.: Seattle, on the University of Washington campus, 17 Sep 1967, Simpson 370 (US).
6. Amaranthus retroflexus L., Sp. Pl. 991. 1753. Type: "Habitat in Pensylvania"; LINN 1117/22.

Annual with erect stem, up to $1.5(-2) \mathrm{m}$. Cotyledons lorate (oblong, ratio 6:1, see Hickey 1978) $13 \times 2-2.5 \mathrm{~mm}$, with acute apex and cuneate base; petiole $5-6 \mathrm{~mm}$ long. Plant scurfy-villous in and for some distance below the inflorescence, both multiseriate and uniseriate trichomes present. Leaves ovate or rhombic-ovate, $3-7 \times 2-4 \mathrm{~cm}$, usually coarsely pubescent beneath, at least along the veins. Inflorescence usually with many short, thick and crowded branches, the terminal part about as long as the laterals. Bracteoles (2.5-)4-6(-8) mm, 1-3 times longer than the tepals. Tepals $5, \pm$ outcurved $2.5-3 \mathrm{~mm}$ long, linear-cuneate to spathulate, rounded, truncate or emarginate, usually mucronate at the tip, of ten with inconspicuous or pale mid-veins. The tepals much longer than the fruit. Fruit circumscissile, about 2 times longer than wide, obovoid, gradually narrowed toward the stigma region. Dehiscence line in the upper part of the fruit, coarsely wrinkled above the dehiscence line. Type of pericarp surface variable, A to B (Fig. 1 B). Seeds obovate 1.1-1.25 $\times 0.8-0.9 \mathrm{~mm}$, lenticular. Between the hilum and the radicle a furrow extends almost to the middle of the seed. The seeds are differentiated into a central, smooth zone and a marginal, sculp-
tured zone. Color dark-brown to black, uniform. Pollen grains 20-27 $\mu \mathrm{m}$, with $30-42$ pores of $1.1-1.4 \mu \mathrm{~m}$ in diameter. Density of granules high. $2 \mathrm{n}=34$.

Usually A. retroflexus offers no identification problems, yet we have encountered interesting specimens sharing the characteristics of A. retroflexus and A. powellii, but somehow different from both. These plants seem to belong to a distinct type that occurs in the dry mountains of Arizona and southern California. They resemble Amaranthus $\times$ tucsonensis recently described by Henrickson (1999) from Arizona. Henrickson suggests only one of the parentsA. hybridus. In our opinion, based on the description and illustration, the flowers are closer to A. retroflexus var. delilei (Richt. \& Lor.) Thell. but the general habit indicates A.powellii. Unfortunately, we could not examine neither the type nor the specimens cited in the study. The plants we examined are fertile, suggesting that they are not Fl hybrids and further research will be necessary to clarify if they are only a variety of A. retroflexus or a stabilized hybrid. Examples:
ARIZONA. Apache Co.: White Mountains, 10 mi S of McKays Peak, 2270 m, 31 Aug 1948, Gould \& Robinson 4998 (ARIZ). Navajo Co.: Pinaleno Mountains, West Peak, 2600 m, 12 Sep 1989,Mc Laughlin 5809 (ARIZ); s.l., 2660 m, 6 Sep 1944, Darrow et al. 1179 (SMU). Snow Flat, 2600 m, 6 Sep 1944, Darrow et al. 1178 (SMU). N of Grasshopper Ruin, 28 Aug 1971, 1800 m, Bohrer 1496 (ARIZ). Gila Co.: Sierra Ancha Wilderness Area, 2000 m, 21 Sep 1991,Imdorf 271 (ARIZ).CALIFORNIA. San Bernardino Co.: San Bernardino Mountains, $116^{\circ} 55^{\prime}$ W, 34ํ $11.25 \mathrm{~N}, 1590$ m, 18 Sep 1994, Sanders 15690 (UCR, ARIZ). NW Shore of Baldwin Lake, $116^{\circ} 49.11 \mathrm{~W}, 36^{\circ} 16.53 \mathrm{~N}, 2043 \mathrm{~m}$, Sanders \& Helmkamp 19489 (UCR).
Distribution and Ecology.-This plant is a native of North America, but has become a cosmopolitan weed.

## APPENDIX 1

Representative accessions cultivated in Rodale Germplasm, Ames, Iowa between 1984-1989, deposited at NA.

## Amaranthus caudatus

USA. AMES 5125,5127,2191, 2212, 2213.PERU.PI 490437, PI 490438, PI 490439, PI 490440. INDIA. PI 166107, PI 175039, PI 166045, PI 480576. NEPAL. AMES 2079, 2165, 2168, 2169, 2182, 2190, PI 427224, PI 427225, PI 427228.

## Amaranthus cruentus

CANADA. (Montreal) AMES 5327.USA. AMES 2264,3216;California, San Rafael, AMES 5165. MEXICO. Chapingo, Inia, AMES 5548; Puebla, AMES 5638, 5640; Sonora, San Bernardo, AMES 5320. GUATEMALA. Choatalum, AMES 5271,5275; San Pedro Corcha, AMES 5269; Aldea Choatalum, AMES 5272, 5273, 5276, 5277 (type 2); Chimaltenango, AMES 5330; Guatemala City, AMES 5278, 5279 (type 1); Coban, AMES 5270, 5279 (type 2), 5298; Chimaltenango, San Martin, AMES 5299;PI 433228, PI 490658, PI 451825, PI 451826; AMES 5676; PERU. Ayacucho, AMES 5346. PORTUGAL. Evora, AMES 5649. CHINA. AMES 1981, 2016, 5313, 5327. INDIA. R-129 A-2250, Spjut 8809; PI 288278, PI 274280, PI 288281; AMES 2037, 2228; Coimbatore, AMES 1977, 5386. NEPAL. PI 490656; Pokhara, AMES 2089, 2092; Chauri Jari, AMES 2061, 2089. MALYSIA. AMES 2054. TAIWAN, AMES 1991, 1992, 2201. INDONESIA. AMES 2042, 2049, 2044. ETHIOPIA. AMES 2003. ZAMBIA. PI 494768, PI 494769. GHANA.

# AMES 1959, 1961, 1963, 1968, 1969, 1970, 1971, 1978, 2006, 2008, 2011, 2012, 2013. BENIN. AMES 5108. NIGERIA.AMES 1973,2055,2056,2057,2058,2250.TANZANIA. AMES 1979,2004.ZAIRE. North Shaba Province, AMES 5369.DAHOMEY. AMES 1964,2000,2249 (type 1 and 2). ORIGIN UNKNOWN. AMES 1985, 2081, 2087, 5151, 5303, 5362, 5384, 5686. 

## Amaranthus hypochondriacus

USA. AMES 2211, 3079, 3078, 5140; Pennsylvania, AMES 8271, 8404; Pennsylvania, K-254; PI 477917 MEXICO. Tulyehualco, AMES 2260;PI 490753;San Miquel, Chiconcuac, AMES 5474;Huazulco, Morelos AMES 5190, 5503, 5637; Oaxaca, AMES 5215; Jautetelco, Morelos, AMES 5503, 5505; Distr Federal, AMES 5499; Chapingo, AMES 2085 (type 1 and 2). CHILE. AMES 5355. PERU. Lima, AMES 7600. AFGHANISTAN. AMES 5610. INDIA. Coimbatore, AMES 1976; PI 274276, PI 274278, PI 274279, PI 480752, PI 480787, PI 480790, PI 480791, PI 480793, PI 480796, PI 480797, PI 480798, PI 480799, PI 480800, PI 480804, 480806, PI 480807, PI 480810, PI 480811, PI 480818, PI 480821, PI 480823, PI 480865, PI 480870, PI 480871. Uttar Pradesh, PI 166045, PI 337611, PI 480814, PI 480815, PI 480819, PI 480820, PI 480866, PI 480872, PI 480874, PI 480875, PI 490756, AMES 2036. Tamil Nandu Agriculture University, AMES 2230, PI 480802, PI 480805, PI 480822, PI 480974. NEPAL. PI 427228, PI 490759; Kathmandu, AMES 2071, 2077 (type 1 and 2), 2162;Patra Sanghu, AMES 2163;Tatopani, AMES 2064, 2160,2167; Chhana, AMES 2173; Charyari, AMES 2061, 2155,2185; Nagma, AMES 2166, 2186;Tibrikot, AMES 2159; Chauri, Jahari, AMES 2086;Khallaged, AMES 2157,2158,2172;Batra, AMES 2178, 2184,2194, 2253;Rodlkhola, AMES 2175; Delhlkot, AMES 2170; Ranka, AMES 2162;Mahadeb, AMES 2171 (type 1 and 2), 2077;Vid Mahuri, AMES 2176; Rotehala, AMES 2177;Tata Village, AMES 2062; Chauri Jari AMES 2067. INDONESIA. Ames 2043. TANZANIA. AMES 1979. NIGERIA. AMES 1975, 2055, 2256. GHANA. AMES 2001 (Type 2), 2002. ORIGIN UNKNOWN. AMES 5141, 5151, 5152, 5158, 5161, 5163, 2081, 2082, 2088, (Type 2), 5361,5381, 5657, PI 490757.

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